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THE CHEMICAL CONTROL OF LEAF AND BUD EELWORMS *(APHELENCHOIDES* SPP.*)* AND STEM AND BULB EELWORM *(DITYLENCHUS DIPSACI)* ON STRAWBERRIES

By R. S. PITCHER
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UNTIL recent years chemical control of the leaf and bud eelworms and the stem and bulb eelworm has not been feasible and attention has therefore been concentrated on the practice of hygiene and the development of hot-water treatments of planting stock. The latter technique uses the differential heat tolerance of plant host and eelworm parasite. With the strawberry the differential is small and, moreover, heat has to penetrate to the centre of the crown of the runner plant if all eelworms are to be killed. Nevertheless, suitable time-temperature combinations have been found, the most recent recommendations in this country being 115° F. for 7 minutes for stem and bulb eelworm and 115° F. for 10 minutes for leaf and bud eelworms (Staniland, 1953).

First attempts at chemical control of these eelworms were made with methyl bromide. This, while successful as a fumigant against the resting stages of stem and bulb eelworm on seeds of onion and other plants, proved to be too phytotoxic for use on strawberry runners (Dicker, unpublished ; Lindhardt, 1950). Soil-watering with sodium selenate solution proved effective against *Aphelenchoides ritzema-bosi* on chrysanthemums (Dimock, 1944 ; Fraser, 1947), but its persistence and high mammalian toxicity make its use undesirable on any cultivated soil and unacceptable on strawberries. Soon after its introduction as an insecticide, parathion was found to show promise as a nematicide against leaf and bud eelworms (Fjelddalen, 1948 ; Sachs, 1950) and in the United Kingdom it has largely superseded hot-water treatment for the control of *A. ritzema-bosi* on chrysanthemums. Other organo-phosphorus compounds, especially demeton, have also been used with some success (Keller and Dimock, 1952 ; Hirschmann, 1953).

Although giving a satisfactory control of the eelworms, hot-water treatment has two disadvantages : it is time-consuming and exacting, requiring special apparatus and skilled operators, and it cannot be used to control an infestation appearing in a crop already growing in the field. Chemical control might meet both these objections and it was with this in mind that the work to be described was started. There were two main phases of investigation. In the first a number of materials, mostly with systemic properties, were selected from the available organo-phosphorus insecticides. These were compared in small-scale pot trials and the mode of action of parathion, the most promising substance, was investigated in greater detail. The second phase comprised the field testing of parathion, used in several different

ways against the three strawberry-attacking eelworms *Aphelenchoides ritzema-bosi* (Schwartz) Steiner, *A. fragariae* (Ritzema Bos) Christie, and *Ditylenchus dipsaci* (Kühn) Filipjev.

POT TRIALS.

Comparative tests of nematicides.

The most frequent of the three species in S.E. England, *A. ritzema-bosi*, was used as the test organism in all the pot trials. Parent plants of the variety Royal Sovereign were planted in the field, inoculated with this eelworm and the runners produced by them lifted and planted in 4-inch pots. For each trial a uniform sample of plants, usually about 9 months old, was selected, randomized and divided into replicates. Parathion, which preliminary tests had shown to be an effective nematicide on strawberries, was used as the standard throughout. In Trial (*a*) toxicants were prepared from purified substances ; the schradan and mipafox were applied in aqueous solution and the parathion and paraoxon dissolved in diacetone alcohol and emulsified with anhydrous *cyclo* hexylamine dodecylsulphate. Commercial formulations were used in subsequent trials ; the parathion and malathion were dissolved in diacetone alcohol and emulsified with a non-ionic agent of the ethylene oxide condensate type and the demeton was a 50 : 50 mixture of the 1952 technical product with an emulsifier of unspecified type. Treatments were applied by adding 50 ml. of the appropriate concentration to the soil. Seepage into the basal crown tissues occurred either immediately or at subsequent waterings, but the toxicant did not wet the foliage at any time. After 4 to 5 weeks the living eelworms were extracted from each plant by stripping the leaf stalks individually from the crown and placing them and the crown in a small Baermann funnel. Because of the large natural differences between the nematode contents of individual plants, the results of these trials were transformed to log $(n+\frac{3}{8})$ for statistical analysis and re-transformed for presentation in Table I.

TABLE I.

Mean numbers of living eelworms recovered from potted strawberries treated with nematicides.

Trial	a			b			c		
No. of replicates	3			5			5		
Concentration of toxicant (%)	0·4	0·1	0·025	0·1	0·05	0·025	0·2	0·1	0·05
Parathion	0	1	2	0	0	1			0
Paraoxon	0	0·3	52						
Mipafox	0	0·7	5						
Schradan	112	97	13						
Demeton				10	27	85			
Malathion							38	135	9
Untreated	28			27			35		

An analysis of variance carried out on the results of Trial (*a*) confirmed that schradan was greatly inferior to the other substances tested, which did not differ significantly amongst themselves at the 0·1 per cent. level. The tests further showed that parathion was superior to schradan, demeton and malathion. Paraoxon and mipafox were about as effective as parathion, but suffered the disadvantage of high mammalian toxicity and were therefore discarded.

Tests of the mode of action of parathion.

It was somewhat surprising to find that parathion, known to be capable of penetrating individual leaves but not of moving readily within the plant, should prove superior to schradan and demeton, which possess systemic properties and might therefore be carried into the central crown tissues, where the bulk of the eelworms live and breed protected by a series of closely overlapping stipules. An attempt was therefore made to find how much, if any, of the nematicidal action of parathion shown in the above tests was due to translocation via the roots. Infested strawberry runners were planted in 4-inch pots as before, but each was surrounded by a 2-inch collar made from a smaller pot, extending about $\frac{3}{4}$ inch above the soil surface and $2\frac{1}{2}$ inches below. By placing the toxicant either on the soil outside the collar or directly on to the base of the plant inside the collar it was possible to differentiate between a true translocation via the roots and a local penetration through the tissues of the crown. In practice the whole 50 ml. dose was given outside the collar for " root " treatments, 40 ml. outside and 10 ml. inside for " root+crown " treatments and 10 ml. inside for " crown " treatments. All routine watering took place outside the collar. Each treatment was replicated seven times and the results, assessed as in previous pot trials, are given in Table II.

TABLE II.

Mean numbers of living eelworms recovered from potted strawberries treated in various ways with parathion.

Trial	Untreated	Concentration (%) and point of application of parathion					
		Root		Root + crown		Crown	
		0·05	0·025	0·05	0·025	0·05	0·025
d	251	195	46	0·5	7	—	—
e	120	1	11	0	5	0·4	0·3

In both trials all treatments differed significantly from the control. In Trial (*d*) the differences between root and root+crown treatments with both concentrations of parathion were significant at the 0·1 per cent. level. In Trial (*e*) all treatments at the concentration of 0·025 per cent. differed significantly from each other at the 5 per cent. level, but at the concentration of 0·05 per cent. no differences were significant. Chemical analysis by the method of Averell and Norris (1948) had shown that small amounts of parathion were present in the open leaves of plants treated at 0·05 per cent. via the roots only. It is therefore possible that translocation of parathion was responsible for the control given by the 0·05 per cent. root treatment in Trial (*e*)

but in both trials there is also ample evidence of nematicidal action by a local penetration of the crown tissues. From these results alone it is not clear whether this is accomplished by a seepage of the diluted emulsion between the ensheathing stipules or is due to a penetration of the active ingredient by other means, but it is clear that, given an adequate concentration of parathion, a thorough wetting of the basal tissues of the plant is all that is needed to obtain a substantial control of *A. ritzema-bosi* on strawberry runner plants.

FIELD TRIALS OF PARATHION.

Against A. ritzema-bosi.

Preliminary field trials had indicated that spring treatment with parathion at 0·025 to 0·4 per cent. considerably reduced the infestation of maiden plants, whether the toxicant was applied as a soil drench at about 1 pint per plant, as a thorough spray, or as a pre-planting runner dip. At the lowest concentration, symptoms began to reappear after 12 months ; at 0·05 and 0·1 per cent., control was satisfactory and free from serious phytotoxicity ; at 0·4 per cent., many plants were killed.

A series of more comprehensive trials of the commercial preparation of parathion used in pot trials (*b*)–(*e*) was therefore begun. The first was planted in the autumn of 1952 with virus-free Royal Sovereign runners raised from eelworm-infested parent plants. Treatments were made as follows at a concentration of 0·05 per cent. active ingredient :

RD, runners dipped before planting
AM, plants sprayed in autumn 1952
SM, plants sprayed in spring 1953
} with about ⅔ pint per plant
AI, plants sprayed in autumn 1953
SI, plants sprayed in spring 1954
} with about 1 pint per plant
U, untreated.

Details of timing are given in Fig. 1. Each treatment was replicated six times on plots of 24 plants each. The short- and long-term effects of these treatments both on eelworms and on plants were obtained by recording eelworm symptoms annually in spring and autumn over a period of 2½ years. Each plant was closely examined and recorded as " clean " unless at least one undoubted eelworm symptom was present. Generally, feeding areas were used as the diagnostic symptom, but occasionally alaminate leaves or enations were accepted as proof of infestation.* Such symptoms can be seen most readily in the spring, but they do not invariably appear on all infested plants, so the figures given, although comparable, are possibly under-estimates of infestation. In Fig. 1 the eelworm records are presented graphically to indicate the changing levels of infestation throughout the life of the trial. The plants were deblossomed in 1953, but in 1954 and 1955 yields were recorded and samples of fruit examined chemically for parathion residues. Table III compares crop yield and the current level of eelworm infestation.

The eelworm records may be summarized as follows :

1. All treatments brought about an immediate and considerable reduction in the severity of infestation.

* See Crosse and Pitcher (1952) for descriptions of these symptoms.

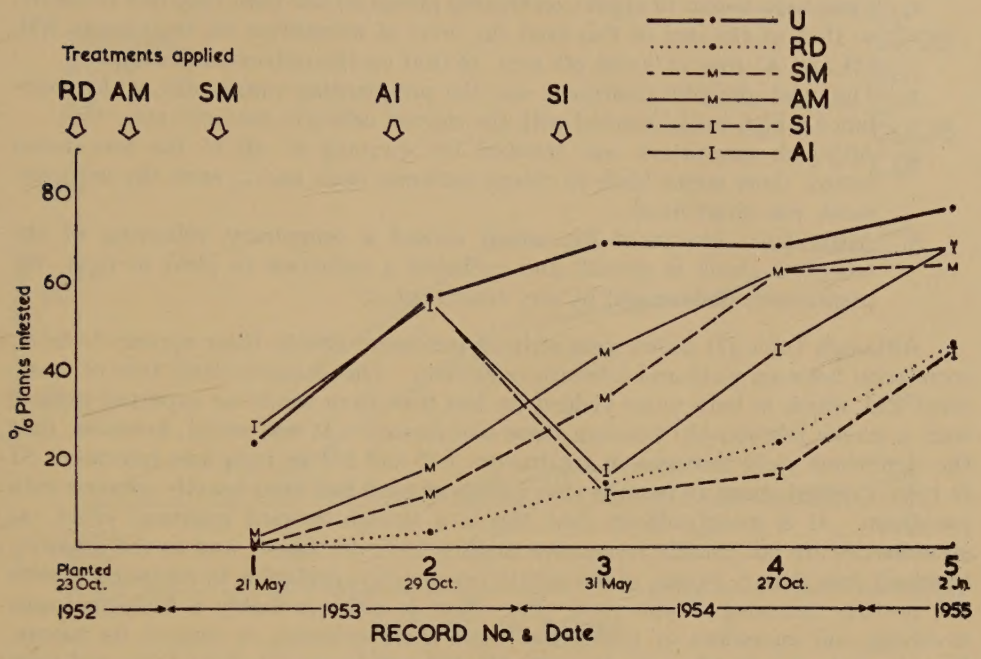

FIG. 1.

Results of parathion treatments (see text) applied to Royal Sovereign strawberries for the control of *Aphelenchoides ritzema-bosi*.

TABLE III.

Trial 1. Comparison of increase in yield and reduction in eelworm symptoms, both expressed as a percentage of the corresponding figures for untreated plants.

Treatment	RD	AM	SM	AI	SI
1954					
Yield increase	37*	48*	54*	16	−6
Eelworm reduction (record 3, Fig. 1)	81*	37*	52*	79*	84*
1955					
Yield increase	2	10	8	10	25†
Eelworm reduction (record 5, Fig. 1)	42‡	10	17	9	44‡

* Significant at 0·1% level
† ,, ,, 5% ,,
‡ ,, ,, 1% ,,

2. Symptoms began to appear on treated plants sooner than they had formerly, so that at the end of this trial the level of infestation on treatments AM, SM and AI rose to 80–90 per cent. of that on the untreated plants.
3. The most effective treatment was the pre-planting runner dip, which combined a high initial control with the slowest eelworm recovery rate.
4. Although infestation was checked by spraying at all of the four times tested, there seems little to choose between them and in each the improvement was short-lived.
5. Apart from treatment SI, which caused a temporary yellowing of the foliage, a check in growth and probably a reduction in yield in 1954, the plants were undamaged by any treatment.

Although Table III shows some striking treatment effects, there appears to be no correlation between yield and eelworm reduction. This is particularly true of treatment RD, which in both years yielded far less fruit than would be expected if there were a simple relationship between these two factors. It was noted, however, that the significant yield increases in treatments AM and SM in 1954 and treatment SI in 1955 occurred about 12 months after plants and soil had been heavily sprayed with parathion. It is most unlikely that this is a straightforward manurial effect, as strawberries are not usually responsive to phosphatic fertilizers, and as the quantity involved (less than 0·25 gm. of phosphate per plant) is negligible in comparison with the routine manuring of the plot. The effect is more probably a biological one, involving soil microflora or fauna, but there is no evidence to suggest its nature. Samples of fruit taken from treatments AM, SM and U on 15th June 1953, and from treatments AI, SI and U on 28th June and 2nd and 5th July 1954, were examined chemically by the method of Averell and Norris (1948), but no parathion residues could be detected, even in plants which had been heavily sprayed about 10 weeks previously.

Pre-planting runner dips had also proved successful in a small trial, concurrent with Trial 1, in which spring dips of 0·025, 0·05 and 0·1 per cent. parathion were tested on eelworm-infested Royal Sovereign runners. All concentrations were effective and non-phytotoxic, but the control given by the lowest concentration was unsatisfactory, falling to about 50 per cent. 18 months after planting. Runner dips were therefore further tested in Trial 2 and the results are illustrated in Fig. 2. Twelve-plant plots and six replications were used to compare the effects of two concentrations of parathion (0·05 and 0·1 per cent.) on autumn-planted strawberries of two varieties, Royal Sovereign and Climax.

The findings of previous trials were confirmed on Royal Sovereign, and parathion at 0·1 per cent. proved safe and effective on Climax. At 0·05 per cent., however, the rate of reinfestation was high on Climax, reaching 45 per cent. of that of the untreated plants $2\frac{1}{2}$ years after treatment and there was some injury by the 0·1 per cent. treatment to the variety Royal Sovereign, 21 per cent. of which died in the first winter, compared with 10 per cent. of the untreated plants.

Against A. fragariae.

Treatments showing promise against *A. ritzema-bosi* were tested against *A. fragariae*, a species rather rare in S.E. England, but common in S.W. England and in Scotland and Ireland. Virus-free Royal Sovereign runners raised from infested

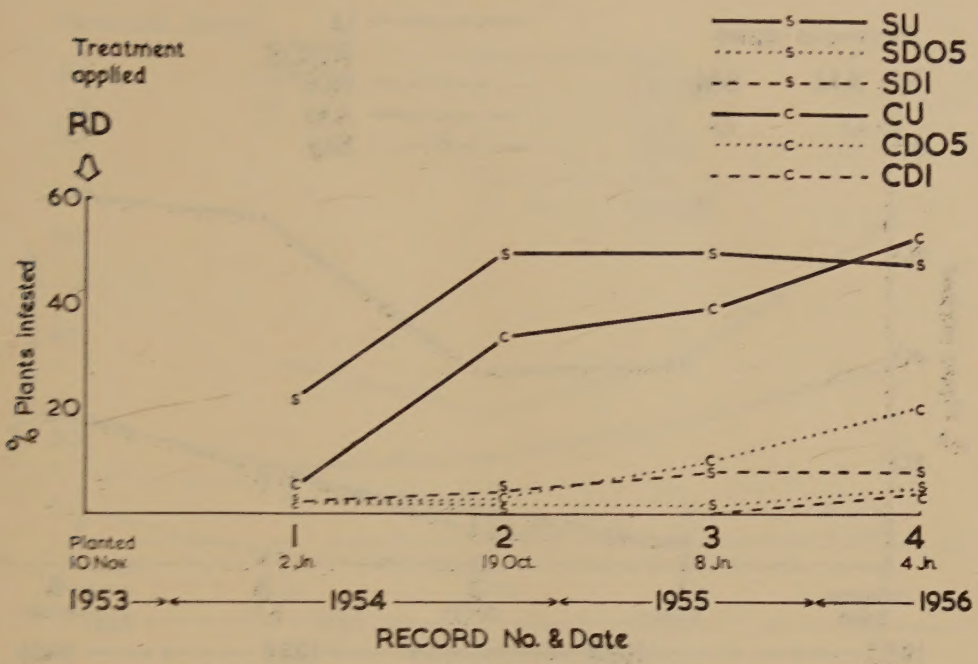

FIG. 2.

Results of pre-planting parathion dips at 0·1 (D1) and 0·05 (D05) per cent. applied to Royal Sovereign (S) and Climax (C) strawberries for the control of *Aphelenchoides ritzema-bosi*. U, untreated.

parent plants were autumn-planted, at twelve plants per plot and eight replicates per treatment. The following parathion treatments were applied :

RD1, pre-planting runner dip at 0·1 per cent.
RD05, pre-planting runner dip at 0·05 per cent.
AM, autumn spray at 0·05 per cent.
SM, spring spray at 0·05 per cent.
U, untreated.

Details of timing and of eelworm infestation, judged by the same criteria as in the *A. ritzema-bosi* trials, are included in Fig. 3.

As with *A. ritzema-bosi*, all treatments gave a considerable and immediate reduction in symptoms, significant at the 0·1 per cent. level, followed by a slow reappearance. Treatment RD1 appeared better throughout than all the others, which differed little amongst themselves. There was no injury to the plants by any treatment.

Against Ditylenchus dipsaci.

The endoparasitic stem and bulb eelworm might be expected to respond less well than the ectoparasitic *Aphelenchoides* spp. to superficial applications of parathion. However, Goffart (1951) and Henderson and Williams (1955) found parathion

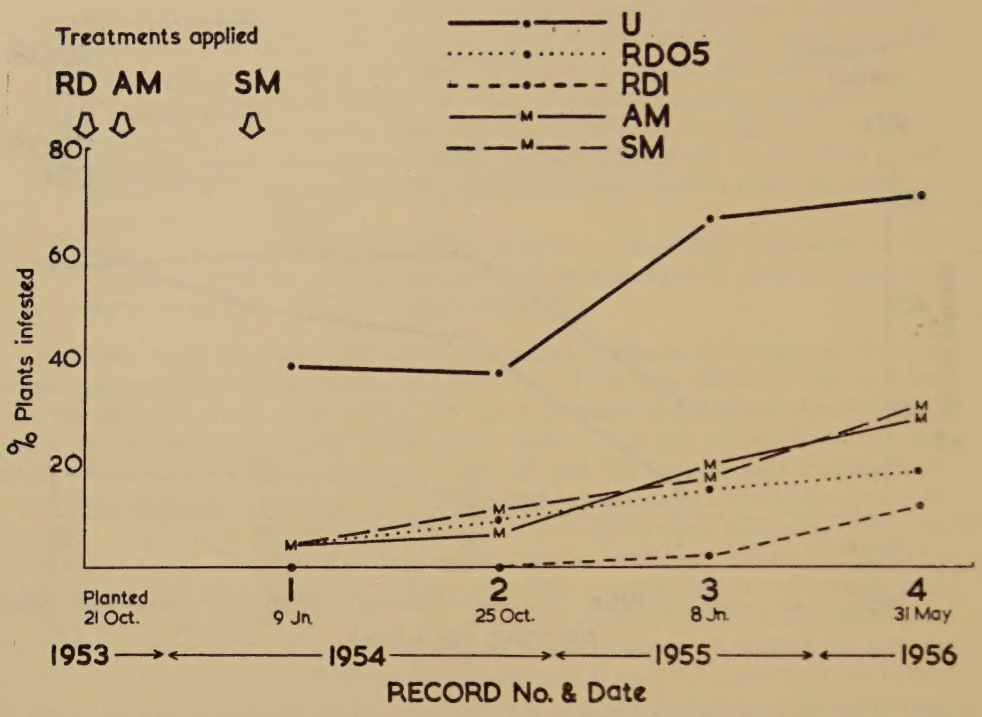

FIG. 3.

Results of parathion treatments (see text) applied to Royal Sovereign strawberries for the control of *Aphelenchoides fragariae*.

effective against this species on agricultural crops, and preliminary field trials showed that spring and autumn sprays and drenches of parathion at 0·05 and 0·2 per cent. controlled stem and bulb eelworm in the strawberry variety Charles Lane for at least 12 months. Accordingly, a longer-term trial was laid down in the autumn of 1953, using runners of the varieties Charles Lane and Mme. Lefebvre raised from eelworm-infested parent plants. Twelve-plant plots were again used and each treatment was replicated six times. The following parathion treatments were applied to Charles Lane, timed as shown in Fig. 4 :

RD1, pre-planting runner dip at 0·1 per cent.
RD05, pre-planting runner dip at 0·05 per cent.
SM, spring spray at 0·05 per cent.
U, untreated.

Because of a shortage of infested planting material only treatments RD05 and U could be applied to Mme. Lefebvre. Eelworm records were taken as shown in Fig. 4, the criteria of infestation being either puckered leaf laminae, swollen petioles or distorted flower trusses. On Charles Lane, runner dips at both concentrations were highly effective, giving an initial control significant at the 0·1 per cent. level and maintaining it throughout the life of the plot. The spring spray did not immediately arrest the development of symptoms and live eelworms could be recovered

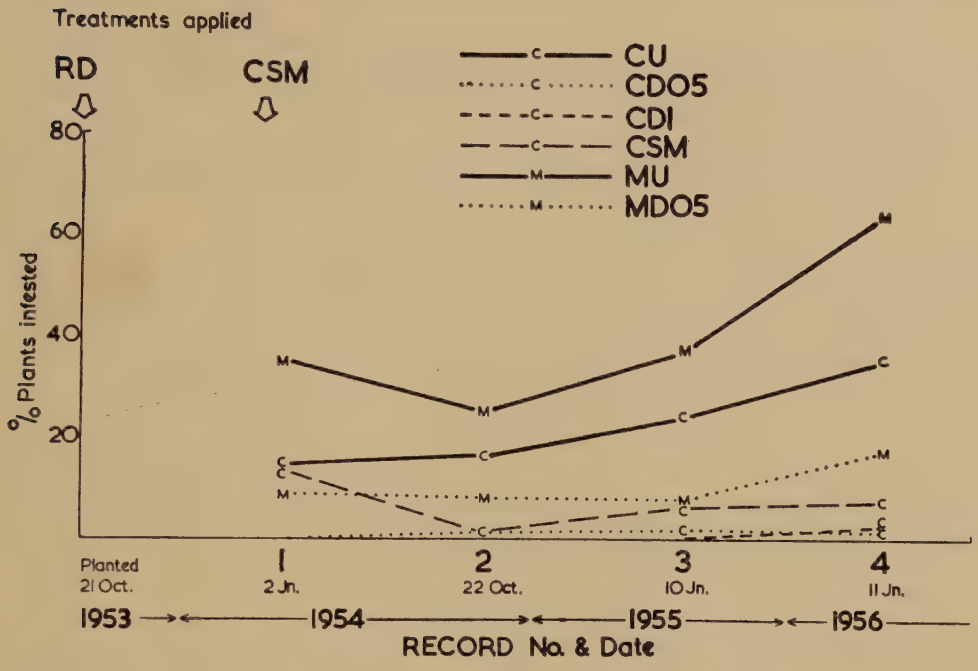

FIG. 4.

Results of parathion treatments (see text) applied to Charles Lane (C) and Mme. Lefebvre (M) strawberries for the control of *Ditylenchus dipsaci*.

from affected petioles at the time of the first record. Later, however, the degree of control approached that obtained by dipping, but it is not known whether this was due to a killing of eggs and larvae, to a slow response of the adults to the parathion, or to an inhibition of reproduction. The variety Mme. Lefebvre responded less satisfactorily to a runner dip, but the eelworm recovery rate remained low.

Phytotoxicity trial.

The above trials clarified the position of parathion as a nematicide and indicated that there was little risk of injury to the four strawberry varieties used. It seemed desirable, however, to test phytotoxicity further before recommending parathion for general use. Autumn or spring pre-planting dips at 0·05 and 0·1 per cent. were therefore tested on runners of six varieties, which were then planted out in eight replications of twelve-plant plots. Survival counts made in the following July showed that no serious injury occurred on any variety, although Royal Sovereign appeared rather more sensitive than the remainder (see Table IV). This variety had previously suffered some damage in a field trial (0·1 per cent. dip in Trial 2), but these plants had already been weakened by severe eelworm infestation. It seems unlikely, therefore, that parathion dips of the concentrations tested will cause serious injury to commercial samples of strawberry runner plants.

TABLE IV.

Phytotoxicity Trial. Numbers of healthy plants, expressed as a percentage of those surviving in untreated plots in July, following a parathion pre-planting dip.

Treatment time and concentration	Royal Sovereign A	Royal Sovereign D	Climax A	Climax D	Mme. Lefebvre A	Huxley A	Perle de Prague A	Cambridge Profusion U
Autumn 0·05%	89	88	98	97	98	93	100	100
Autumn 0·1%	84	90	99	95	95	97	93	103
Spring 0·05%	104	97	102	93	98	100	104	98
Spring 0·1%	96	91	100	99	96	97	102	98

A, infested by *A. ritzema-bosi* ; D, infested by *D. dipsaci* ; U, uninfested.

DISCUSSION AND CONCLUSIONS.

With all three eelworm species the apparent level of infestation of untreated plants rose steadily throughout their life. Probably there are three major factors which determine the rate of increase, namely :

(*a*) plant-to-plant spread amongst strawberries,
(*b*) plant-to-plant spread from weeds to strawberries,
(*c*) a gradual increase of the eelworm population of individual strawberry plants to, or beyond, the level at which symptoms appear.

These three factors may act separately or in combination, but without detailed biological data it is impossible to say which is the most important.

All treatments rapidly reduced the symptoms produced by all three eelworm species. In the case of the stem and bulb eelworm this improvement was maintained for a further two years but, in plants infested with either species of leaf and bud eelworm, symptoms began to return after 6 to 12 months and this trend continued steadily and sometimes rapidly throughout the remainder of each trial. As with untreated plants, there is insufficient evidence to determine the mechanism of this increase, but the form it took, especially in Trial 1, suggested a build-up of a residual population from within the plants rather than a reinfestation from without. With all three species, pre-planting dips gave an immediate and more lasting control than the spraying of established plants in the field.

It is therefore clear that, although eelworm infestation of established plants can be reduced to some extent by spraying with parathion, the practical applications of the technique are limited. With the stem and bulb eelworm, where spraying can produce a considerable and lasting improvement in infested plants, although not in infested soil, it may be worth while ; with the leaf and bud eelworms, the rapid reappearance of symptoms makes it of doubtful value. Repeated spraying would probably keep symptoms down indefinitely, but the high cost (£12–£25 per acre per application for materials alone) would not be economic. Moreover, the repeated use of heavy doses of parathion on strawberry plants might result in residues that were toxic to the consumer (David and Aldridge, 1957).

While there is no doubt that the planting of eelworm-infested or suspect strawberry runners is unwise, circumstances may sometimes compel their use. In such a case, parathion pre-planting dips offer a practical means of control. They are less

costly than sprays and entail less risk to operators and none to the consumer. Because they also control aphids the routine nicotine pre-planting dip can be omitted. As eradicants they are rather less efficient than hot-water treatment, but are much simpler to carry out and certainly no more harmful to the plants. A concentration of 0·1 per cent. of the active ingredient (8 oz. of a 20 per cent. concentrate to 10 gallons of water) is recommended, and full precautions must be taken to avoid contamination, especially of hands and face, during dipping and planting operations.

SUMMARY.

An account is given of preliminary laboratory testing of a number of substances as nematicides, using the eelworm, *Aphelenchoides ritzema-bosi*, as a test organism, and of extensive field testing of parathion against this species and *A. fragariae* and *Ditylenchus dipsaci*. With each species the level of infestation was greatly reduced by parathion, whether used as a drench, a spray or a pre-planting dip ; with *Aphelenchoides* spp., symptoms gradually reappeared over a 3-year period. Of the control measures tested, a pre-planting dip in parathion at 0·1 per cent. active ingredient gave the best results.

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THE RESPONSE OF APPLE STEMS TO WOUND INFECTION BY *GLOEOSPORIUM PERENNANS*

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Gloeosporium album and *G. perennans*, the two fungal species mainly responsible for losses of stored dessert apples, normally overwinter in the orchard as tree infections. Both exist saprophytically on small dead stubs and mummified fruitlets (Guthrie, 1957) ; in addition, *G. perennans* infects living shoots through wounds, inducing conspicuous parasitic canker and die-back infections (Wilkinson, 1945) (Fig. 1). *G. album*, on the other hand, only rarely forms extensive lesions on Cox trees.

In this country, studies of the wood infection stage of the disease have so far been mainly concerned with seasonal variations in susceptibility of certain types of wounds to *Gloeosporium* spp. and with factors affecting spore dissemination from the resulting lesions (Corke, 1956). This paper† deals specifically with the anatomical development of canker and die-back infections which were artificially induced, on trees carrying no natural infection, by pure culture inoculations with *G. perennans* ; the lesions were then examined at selected stages of development.

Materials and methods

The morphological studies were made with shoot infections which had been artificially induced at intervals of 3–6 weeks from October 1955 until January 1957 on 20-year-old bush trees of the variety Cox's Orange Pippin, planted in a 30-ft. quincunx. On each occasion at least 30 replicate shoot infections were established on 1–3-year-old branches by inoculating pin-stab wounds with mycelium from a tube-culture of *G. perennans* ; in addition, 20 pruning wounds were inoculated with a conidial suspension of *G. perennans* (50,000 spores/ml.). Ten control wounds of each type were left without fungal inoculum. The inoculum was protected for 20 days by a strip of self-adhesive crêpe rubber. The resulting lesions were collected at intervals of 2–6 weeks, depending on the season and on the age of the different sets of infections. Normally one lesion in each set of inoculations was collected on each occasion and routine collections were continued until October 1957. The fresh material was either fixed in formalin-aceto-alcohol and stored in 50 per cent. alcohol, or fixed and softened by boiling in water for 20 minutes, followed by soaking for 3 days in a mixture of equal parts of glycerine and methylated spirits, and then stored in a mixture containing 10 parts glycerine and 90 parts methylated spirits. Sections from 5 to 12 μ in thickness were cut with a sledge microtome from material

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PLATE I

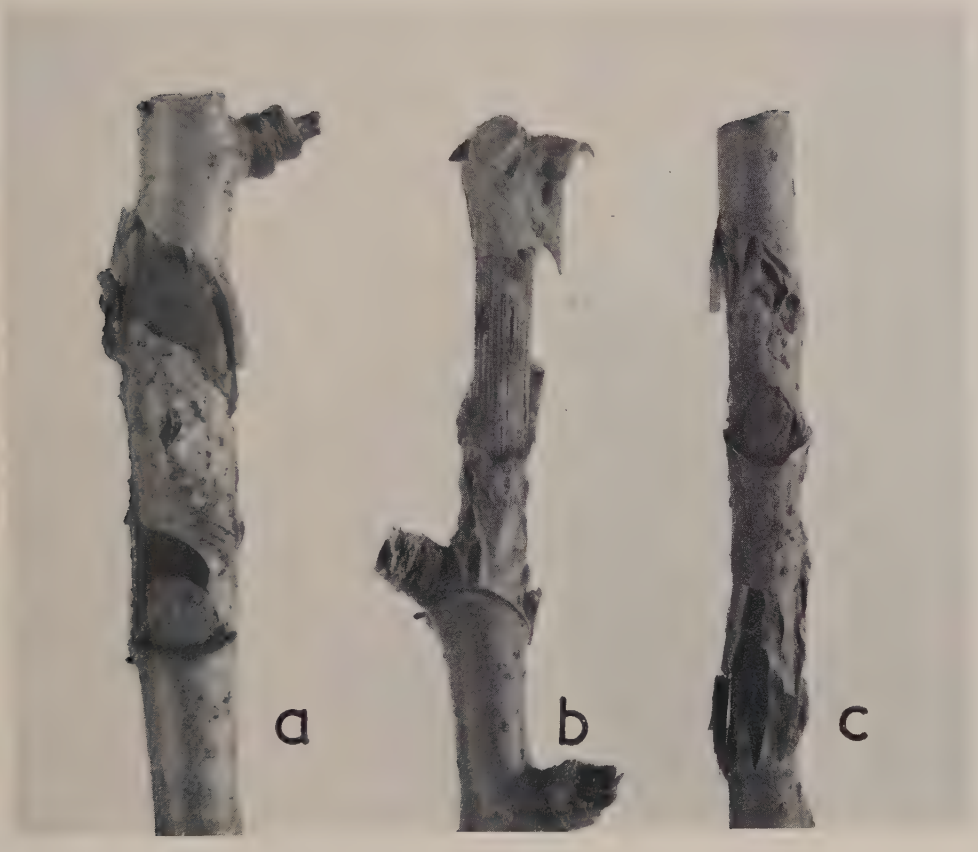

Fig. 1.

Seven-month-old infections of *G. perennans* on Cox shoots, artificially induced during November in wounds of three different types: (*a*), pin-stab wound; (*b*), terminal pruning wound; (*c*), lateral pruning wound.

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embedded in paraffin wax, while sections up to 20μ in thickness were cut without embedding with a freezing microtome. The sections were stained in safranin and picroaniline blue (Crowdy, 1949).

LESIONS ARISING FROM PIN-STAB WOUNDS INFECTED WITH *G. perennans*.

For convenience, the results under this heading are grouped into two series. Series I consists of infections initiated during dormancy and Series II of very small lesions initiated just before or during the season of host activity. In each series the healing process of uninfected wounds will be considered before describing the development of shoot infections.

Series I. Wounds made between 21st October 1955 and 17th January 1956. Healing of uninfected wounds.

A week after wounding, resinous globules were apparent in the cells lining the injured peripheral tissue and in the ray and parenchymatous cells of the xylem adjacent to the wound. Within 5 weeks the zone of gummed parenchyma extended for about ten cells around the wound in the bark and within a 1·7-mm. radius of the wound in the xylem ; in addition, small amounts of amorphous gum were deposited at the perforations of some vessel segments. A phellogen was initiated in the healthy peripheral tissues adjoining the gummed zone and this produced a double layer of cells which subsequently became suberized and continuous with the original periderm. Thus, 6–8 weeks after wounding in late October, the damaged peripheral cells and some immediately adjacent tissue were isolated (Fig. 2). Wounds of the November series were not isolated, however, until 10 weeks after initiation and phellogen production was delayed even later in the December series. The wounded tissue remained in this condition throughout the rest of the dormant season.

In 1956 bud burst occurred about mid-April and, from the end of March onwards, amorphous gum was deposited in the xylem vessels bordering the zone of gummed medullary rays until, by the end of May, these vessels were completely blocked.

During early May healing recommenced with the proliferation of parenchymatous callus from the inner face of the phellogen ; production of this tissue was particularly rapid in the phloem region. In the undamaged tissues the vascular cambium became active and, since those cells adjacent to the wound divided less frequently, the cambium became recurved (Fig. 3).

During June and July the recurved cambium extended by radial divisions to form a meristematic arc which was continuous with the inner zone of the phellogen. Thus the callus tissue was produced from two meristems : an outer zone of parenchymatous tissue, produced by the phellogen, surrounding an inner zone of hard tissue (wound wood) composed of slowly lignifying, iso-diametric, thick-walled cells derived from the recurved cambium. The cambium external to the wound wood apparently produced normal phloem, while the wound wood itself gradually merged into normal xylem.

Swarbrick (1927) showed that the most rapid development of callus, after bark ringing, takes place between mid-June and mid-July and is correlated with the beginning of starch re-deposition and the attainment of the full-leaf stage in the tree. This author also noted the part played by the phellogen in callus production.

Sass (1932) has shown that callus tissue produced in the formation of graft unions in apple is derived exclusively from tissues outside the xylem cylinder, apart from phelloderm. Since the latter tissue normally comprises three layers, including a phellogen, it should be pointed out that Sass referred only to the superficial meristem external to the cortex and not to a wound phellogen extending down through all the peripheral tissues to the xylem as described here.

Ingrowth of the callus continued until by mid-August the edges fused and the

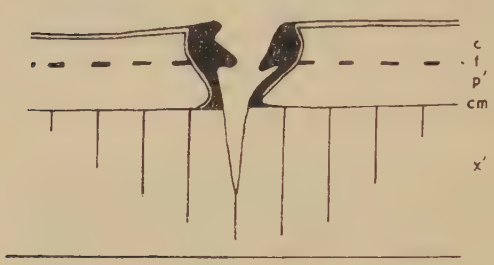


Fig. 2

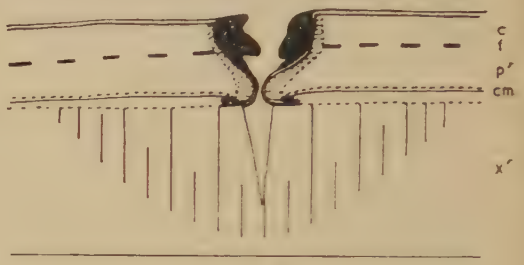


Fig. 3

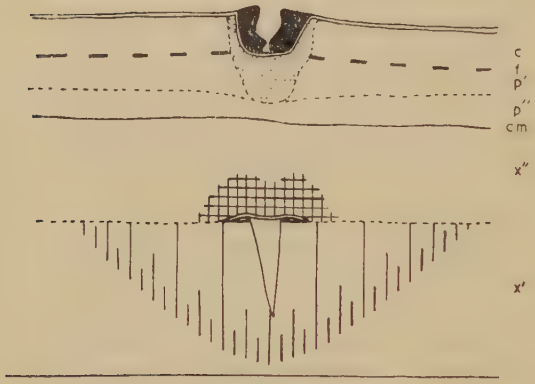
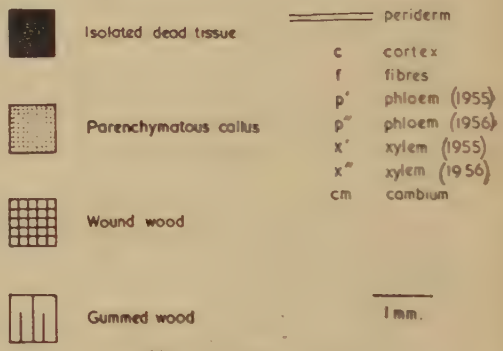


Fig. 4



Key to Figs. 2–4

FIGS. 2-4.

Diagrammatic longitudinal sections illustrating main stages in healing of uninfected pin-stab wounds on apple shoots, initiated on 21st October 1955. Fig. 2, collected 1st December; Fig. 3, mid-May; Fig. 4, mid-August.

cambium cylinder was completely restored and was producing normal vascular tissue external to the wound wood. Most of the isolated peripheral tissue was sloughed off above the callus but a small amount of the remaining secondary phloem was gradually crushed by the overlying callus (Fig. 4).

Development of shoot infections from inoculated pin-stab wounds.

Shortly after inoculation, mycelium grew from the agar on to the injured surface of the bark, and in 2 weeks the septate hyphae were found in lateral disruptions of the soft peripheral tissue and in the sieve tubes and vessels bordering the wound.

Fig. 5 shows the situation between 3 and 4 weeks after inoculation. Hyphae were growing between the gummed cells of the cortex and along the lumen of the sclerenchymatous fibres of the inner cortex ; the fibre infection was occasionally found up to 1·5 mm. in advance of the infection in the parenchyma. In the phloem, hyphae grew strongly through the sieve tubes and occasionally between the companion cells. Resinous globules occurred in the cortical parenchyma and in the phloem ray and companion cells a few cells behind the most advanced hyphae. Strongly-growing, branched hyphae had also spread along the vessels and occasionally through the fibres of the outer zone of the secondary xylem, but penetration of the ray and wood parenchyma cells was only occasionally observed at this stage. Resinous globules were produced in the wood parenchyma and ray cells of the infected xylem and, although sporadic deposits of amorphous gum appeared in some of the vessels, no effective mechanical barrier was formed. In contrast to the comparable uninfected wounds already described, the infected wounds made on the 21st October showed no new phellogen development during the winter.

Fig. 9 shows that transverse spread of the infection was uniform through all the invaded tissues. On the other hand, longitudinal spread occurred more rapidly through the vascular tissue, and especially the outer zone of the xylem, than through the cortex (Fig. 6).

Throughout the dormant season the fungus advanced steadily through the vessels and sieve tubes. In the bark, hyphae continued to spread through the fibres and, although some lesions showed moderate infection of the cortical parenchyma, this tissue remained intact. In March, intercellular hyphae were often noted up to six cells in advance of the zone of gummed peripheral tissue.

By early March 1956, streaks of gummed medullary rays extended through the xylem beyond the limits of the external signs of infection. Hyphae were growing a relatively short distance along the central vessels of these streaks, the edges of which were bounded by vessels containing slight gum deposits.

By the end of March 1956, lesions initiated in the autumn of 1955 had almost girdled the shoot and measured up to 4 cm. in length, with streaks of gum in the xylem extending 5 cm. beyond the external limits of infection. The rate of deposition of amorphous gum in the vessels adjacent to the infected xylem then began to accelerate until, by mid-May, most of the vessel segments bordering the infected xylem had become blocked. No phellogen was seen until the early part of May, when it arose in the healthy peripheral tissues up to 0·5 mm. ahead of the gummed cells (Fig. 6).

Between June and the end of September, further gum deposition occurred in the vessels adjoining the existing barrier. As in the uninfected wounds, the phellogen and cambium produced a healing callus consisting of an inner zone of wound wood covered by an outer zone of parenchymatous tissue (Fig. 7).

In the isolated moribund bark tissues, hyphae formed intercellular aggregates which ruptured the phloem and inner cortex, while, in the outer cortex, the mycelium became intracellular. Hyphae also grew outwards between the peridermal cells and these were quickly followed by aggregations of parallel hyphae which formed acervuli (Fig. 7) : where the periderm had flaked off, acervuli were borne on the surface of the exposed cortex or phloem. The acervuli, which began to appear from May onwards, were normally about 0·5 mm. in diameter and consisted of parallel hyphae ending in branched conidiophores from which spores were abstracted singly.

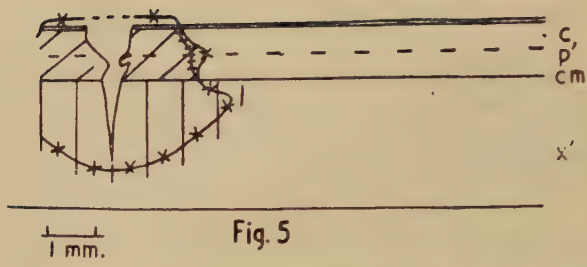


Fig. 5

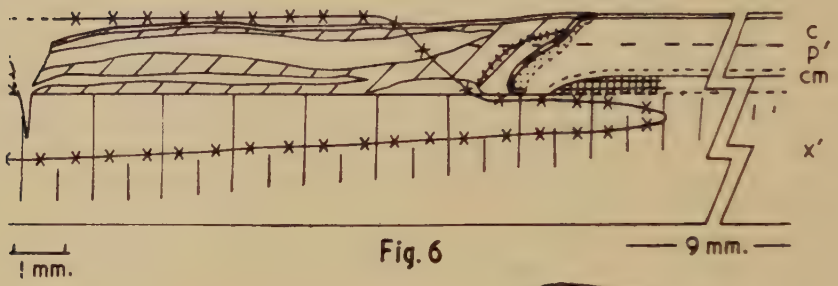


Fig. 6

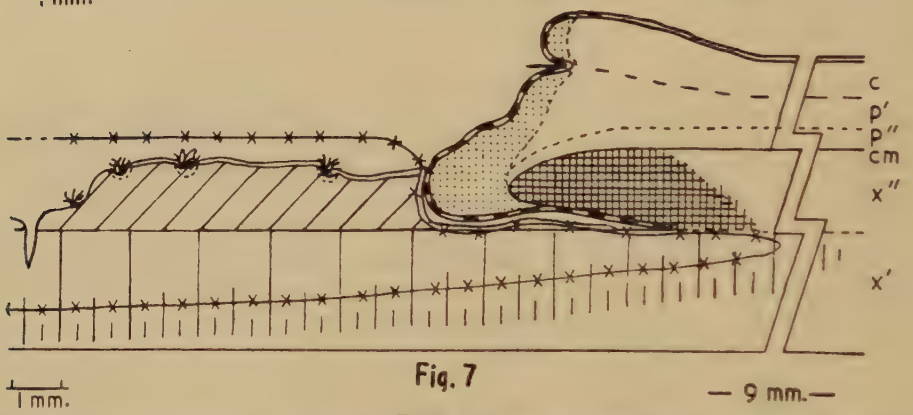


Fig. 7

FIGS. 5-7.
Diagrammatic longitudinal sections illustrating stages in development of pin-stab wound infections of *G. perennans* on Cox, initiated on 21st October 1955. Fig. 5, collected 12th November ; Fig. 6, 11th May ; Fig. 7, 23rd July.

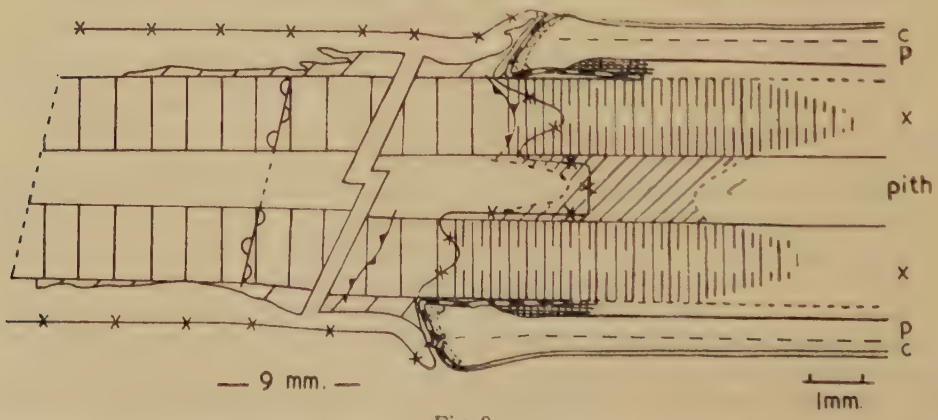


Fig. 8
Diagrammatic longitudinal section of terminal pruning-wound infection of *G. perennans* on Cox ; initiated 17th January 1956, collected 2nd October 1956.

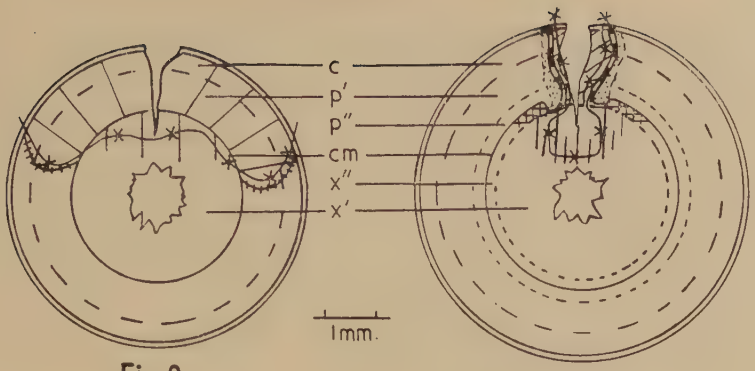


Fig. 9

Fig. 10

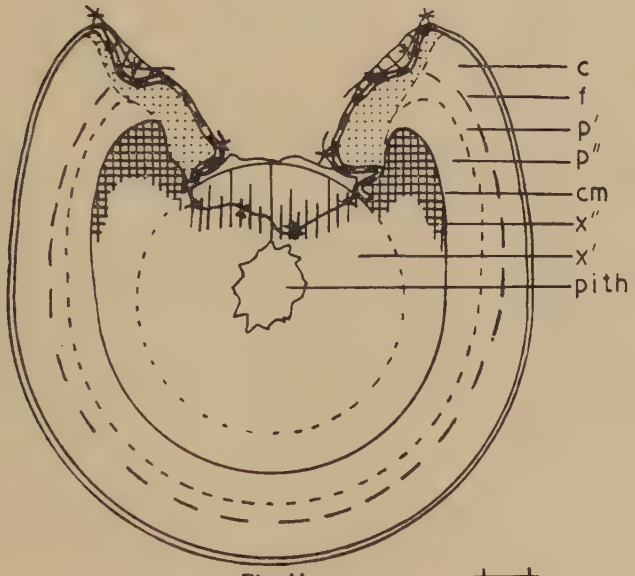
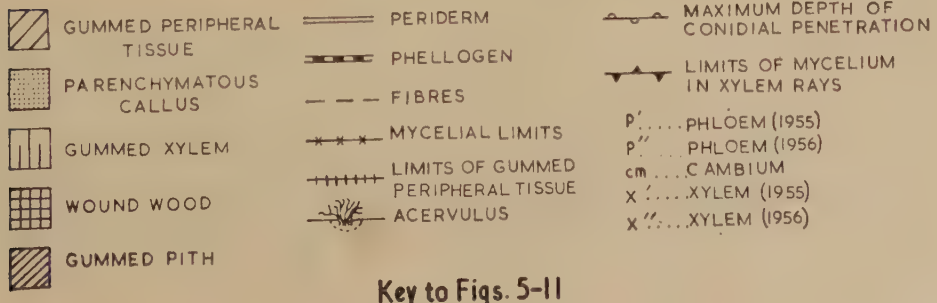


Fig. 11

FIGS. 9-11.
Diagrammatic transverse sections of pin-stab wound infections on Cox. Fig. 9, initiated 15th November 1957, collected 10th January 1958; Fig. 10, initiated 6th April 1956, collected 31st May 1957; Fig. 11, initiated 7th November 1955, collected 30th January 1957.



Key to Figs. 5-11

The fungus continued to exploit the isolated tissue, especially in the phloem and inner cortex, and so caused the remaining relatively intact periderm and outer cortex to flake off. Although, by the end of the summer, a ridge of callus had formed around all the cankers initiated during the previous winter, most of the infected wood was still uncovered.

Little change was recorded in cankers collected during the winter of 1956–57, the limits of infection remaining as imposed during the previous summer (Fig. 11). With the renewal of cambial activity in the following spring, callus production restarted and, as more wound wood was laid down, the callus ridge continued to grow inwards towards the original pin-stab. During 1957, thick wefts of hyphae spread throughout the xylem and invaded most of the ray and wood parenchyma cells. The average conidial output from cankers of this age was about 40 per cent. of that recorded in the previous year.

Anatomical observations of a further series of pin-stab wound infections initiated between 24th October 1956 and 18th January 1957 provided confirmation of the results described above.

Series II. Wounds made between 6th March and 12th October 1956.

Healing of uninfected wounds.

Uninfected pin-stab wounds made in March were isolated by phellogens in early May and by the end of this month vessels adjacent to the wound were completely blocked with gum. Phellogens were produced within 4–6 weeks around wounds made between April and mid-October and, in most of these cases, parenchymatous callus was already developing beneath the phellogen before the wound periderm had been completely suberized. Where wounds were made before September, amorphous gum continued to accumulate until, within about 6 weeks, the damaged wood was isolated by a tier of blocked vessels. In wounds made between 4th September and 12th October, however, this process was not always completed by the end of the season of host activity, so that the zone of gummed wood included several partly-filled vessels. By the autumn all wounds made before July had become occluded by callus ; those made in August and September were only partially covered by this time, however, and no callus was laid down around wounds made on 5th and 12th October 1956 until the following spring.

Development of shoot infections from inoculated pin-stab wounds.

Wounds inoculated with *G. perennans* between March and mid-October 1956 did not develop into infections as severe as those initiated during the period October 1955–January 1956. The final external diameter of the lesions rarely exceeded 1·0 cm., with the region of gummed xylem usually extending for an additional 0·5 cm. beyond the external signs of infection. No acervuli were recorded on lesions of this series.

The initial stages of fungal invasion and host reaction followed the pattern of the earlier series of infections. Hyphae penetrated between, and occasionally entered, the cortical parenchymatous cells but the heaviest infection was again in the fibres, sieve tubes and vessels. In lesions initiated in March, blocking of the vessels was not completed until the end of May but, where lesions were initiated between April and August, the diseased wood was isolated within 6 weeks. Although

occasional vessels surrounding lesions induced in September and early October remained incompletely filled by the end of the season of host activity, spread of mycelium appeared to be prevented as effectively as in lesions initiated during midsummer. The time taken for the appearance of phellogens around lesions initiated between March and August was similar to that for uninfected wounds, but phellogen formation was delayed up to 8 weeks in lesions induced in September and early October. In lesions initiated before October, parenchymatous callus was produced before the wound phellem had become completely suberized and, with the renewal of cambial activity, wound wood was laid down around the edges of the lesion. By the end of the growing season very little of the diseased wood remained uncovered by callus. The distribution of the mycelium, as seen in transverse section in 8-week-old lesions of Series I and II, may be compared by reference to Figs. 9 and 10.

Lesions arising from pruning wounds infected with *G. perennans*.

Shoot infections artificially induced by inoculation of pin-stab wounds with mycelium have been dealt with above (Fig. 1a). Under natural conditions a similar type of injury, caused by apple woolly aphid punctures, may also become infected. More frequently, however, natural infections occur in freshly made pruning cuts (Figs. 1b and 1c) and the anatomical development of infections of this type will now be considered.

No further detailed studies of uninoculated pruning cuts were made as the general pattern of seasonal variations in the healing of healthy pruning wounds was found to be similar to that described by Swarbrick (1926).

Corke (1956) and Sharples (1958a, 1958b) have recently shown that the development of infections of pruning wounds is less closely related to seasonal variations in host activity than is that of pin-stab wounds. The following therefore applies to pruning wounds successfully infected with *G. perennans* at all times of the year, since the general pattern of development was similar, regardless of the final length of the lesion.

Infection of terminal pruning cuts.

This account is based on examination of sections of shoot infections artificially induced in wounds left after a branch had been shortened (terminal pruning-wound infections).

Natural shoot infections are most frequently induced by conidia which are carried in rain water from existing cankers. In artificially induced infections the conidia were drawn into the vessels of freshly made cuts down to a depth of about 2 mm., where germination took place readily (Sharples, 1958b). Within a fortnight, vigorous hyphae had grown down through the vessels and fibres of the xylem and entered the medullary ray cells immediately below the cut surface. The mycelium developed transversely through the rays outwards into the phloem and inner cortex. Thus, although the most advanced penetration was in the xylem, the fungus was also strongly established in the pith, phloem and inner cortex a short distance behind.

Although the mode of extension of established pruning-wound infections was essentially the same as that of pin-stab infections, in the pruned shoot (Fig. 8) the

mycelium continued to spread at a moderate rate through the pith, a tissue which is not normally invaded in pin-stab infections. The fungus also entered the ray cells of the infected xylem in pruning-wound lesions ; infection of these cells in pin-stab lesions of comparable age was generally slight, or heavy only near the centre of the lesion. Host reaction during dormancy was confined to sporadic deposition of amorphous gum in the vessels and to the production of resinous globules in the living parenchymatous cells of the shoot. The mature pith was composed of less responsive cells since they often remained unmodified in the presence of the pathogen.

During the season of host activity, the length of the parasitic phase of extension of terminal pruning-cut infections was determined by the rate of development of suberized barriers in the bark and of gum deposition in the vessels bordering the infected xylem. Resinous contents sometimes occurred in the pith at a position corresponding with the maximum blocking in the vessels. Where the shoot was completely girdled, the phellogen and gum barrier formed obliquely across the shoot in advance of the fungus (Fig. 8). Callus was laid down in the normal way, but at a slower rate than in pin-stab lesions. Once further extension had been arrested, the amount of mycelium increased rapidly in all the parenchymatous tissues of the isolated lesion, including the pith, and acervuli pushed up through the periderm as described earlier.

Comparison of terminal and lateral pruning-wound infections.

Since experiments (Sharples, 1958a) have shown that, during summer, terminal pruning-wound infections are likely to develop into more severe lesions than those initiated in wounds left by excision of a lateral shoot (lateral infections), comparison was made of the distribution of mycelium and the rate of healing in lesions of these two types.

Initially, in both types of infection, the fungus grew down the whole body of the shoot or lateral stump. In terminal infections the mycelium continued to grow evenly through all the tissues of the shoot ; in lateral infections, however, spread of the mycelium became restricted to the vascular tissue and bark of the wounded side of the shoot, but the mycelium in the pith of the lateral stump failed to spread into the pith of the main shoot. It sometimes happened that lateral infections spread transversely until the shoot was girdled, but usually wound barriers were formed before this condition was reached. The amount of wound wood laid down around lateral wound infections, where the distal portions of the shoot were still alive, was similar to that produced around pin-stab infections.

Penetration of infection barriers.

Wilkinson (1945) noted that the spring callus formed around die-back infections of *G. perennans* was not always permanent. In a limited amount of material obtained at Long Ashton, natural reinfection of healthy tissue, behind well-formed wound barriers surrounding lesions of *G. perennans*, was normally associated with broad bands of infected sclerenchymatous fibres passing through the suberized layer formed by the first phellogen. Although the phellogen had formed alongside the fibre band for some distance, the hyphae eventually broke out into the surrounding bark tissue to form a heavy infection extending for about 0·5 cm. in front of a second suberized barrier. Extension of die-back infections rarely exceeded 1 cm. in these cases and appeared to be confined to the bark tissues only.

In contrast to the die-back infections, where natural penetration of the wound barrier may occur, extension of cankers, where healing normally takes place before the shoot is completely girdled, may be induced only by artificially damaging the callus (Wilkinson, 1945). The amount of callus produced around cankers of *G. perennans* is considerably greater than that laid down at the base of die-back infections and, since the parenchymatous callus lacks fibre bundles, the continuity of the infected bark fibres is probably disrupted.

In a number of pruning-cut infections, initiated in July 1957 on 2- to 3-year-old branches, the fungus spread through the infected bark in a series of stages marked by successive phellogens, separated by blocks of infected tissue. The vessels of the infected xylem were only partially blocked. Spread of the infection in this case resembled the general mode of development characteristic of cankers of *Nectria galligena* (Crowdy, 1949).

DISCUSSION.

It has been seen that, in the development of shoot infections of *G. perennans*, the presence of the fungus impedes the natural healing processes by which uninfected wounds are isolated. There is a sharp contrast between the normal healing mechanism in the parenchymatous tissues of the bark and that in the vessels of the xylem. In the bark, suberized barriers around the injured tissues are formed by phellogens ; in the xylem, the barriers are composed of deposits of gum that block the vessels. The rate of formation of these barriers around uninfected wounds is affected by the degree of host activity. Although other factors affect the rate of barrier formation (Sharples, 1958a), in general the most marked differences in rate of healing are associated with seasonal host activity. In uninfected pin-stab wounds, development of effective suberized barriers in the bark takes place about 1–2 weeks more quickly during the spring and summer than during the winter. These well-formed spring and summer barriers are also quickly reinforced by the proliferation of callus, whereas no callus is formed during winter.

The first response of the plant to disturbance of the normal condition within its tissues is the production of resinous globules in the parenchymatous tissues and the deposition of viscous, amorphous gum in the vessels. Swarbrick (1926) has suggested that " wound gums " are first formed in the xylem from starch and possibly other materials within the ray and wood parenchyma cells, and that they later spread to the non-living vessels. Presumably the production of resinous globules would be similarly effected in the living cells of the cortex and it is noteworthy that, during dormancy, only slight gumming occurs in the mature pith cells, most of which are without their protoplasts. Swarbrick also found that sap expressed from apple shoots in the spring and summer showed marked activity for invertase and diastase. It therefore seems probable that effective gum barriers can be laid down only when adequate carbohydrate supplies and suitable enzymes are available ; that is, while the tree is in leaf and the sap is rising.

When apple shoot tissue was wounded and inoculated with *G. perennans*, the presence of the fungus in injured tissue failed to induce any special responses in addition to those recorded in uninfected mechanically-made wounds. The time of response in infected wounds was delayed, however, particularly in winter-initiated lesions and in infections developing on summer-pruned 2- to 3-year-old branches. Crowdy (1949)

has pointed out that the spread of *Nectria galligena* in cankered apple wood depends on the balance between the development of the pathogen and the resistance of the host and, although the spread of *G. perennans* is retarded by low winter temperatures (Corke, 1956), the present studies also show that, broadly speaking, the rate of lesion development is inversely related to the degree of host activity.

The effect of seasonal variations in host activity on the spread of the fungus is illustrated by the studies of pin-stab wound infections. Thus, during the summer, host activity is at a peak and suberized barriers, capable of resisting the diffusion of fungal enzymes, are produced rapidly enough to contain the infection at an early stage. Gum deposition in the vessels also proceeds at a very rapid rate so that spread of mycelium through the wood is likewise prevented. It appears from the work of Crowdy (1948, 1953) that the more rapid production of phellogens in the summer may be associated with a seasonal cycle of auxin production. The site of production of effective wound phellogens would therefore depend on the speed with which the fungus becomes established and subsequently advances, in relation to the speed with which phellogens are produced.

The critical nature of the balance between pathogen and host is illustrated by comparing the small pin-stab wound infections resulting from inoculations made in the middle of October 1956 with those initiated 12 days later ; the latter developed into extensive cankers and were not isolated until the following spring.

Between late October and the following March, it appears that the host is unable to form barriers sufficiently quickly to prevent the spread of *G. perennans* after the inoculation of freshly made pin-stab wounds. At that time, however, and even during dormancy of the host, phellogens are produced in uninfected wounds at a comparatively slow rate and Sharples (1958b) has shown that pin-stab wounds made in November had become immune from infection by mycelium of *G. perennans* within 3 weeks. Wiltshire (1921, 1922) also showed that, during the winter, the successful establishment of wood infections of *N. galligena* depends upon the speed with which the host responds to form a limiting phellogen.

Fungal invasion of the different tissues of the shoot occurs in two phases : first, a parasitic phase in which the lesion extends ; second, a saprophytic phase which begins when further spread has been checked and in which the mycelium develops strongly in the isolated zone. These two phases will now be considered.

Parasitic phase of infection.

Gloeosporium infections, initiated in the late autumn, extend steadily during the winter. This stage corresponds to the parasitic phase noted by McLarty (1933), in which the most rapid spread of the fungus occurs through the vessels, wood fibres and sieve tubes, elements characterized by a paucity of contents and absence of cross walls. In contrast, *G. perennans* spreads relatively slowly between the closely packed cells of the collenchyma and at only a moderate rate through the intercellular spaces of the less compact inner cortex. The fungus appears unable to occupy living cells directly and only becomes generally intracellular some time after the cell has been passed by the mycelial tips. In the early stages of pruning-wound infections, the mycelium probably spreads transversely from the infected vessels out into the peripheral tissues by way of the medullary rays. At this stage, intracellular infection of the pith tends to advance only slowly.

Many of the artificially induced pin-stab infections, examined 3 weeks before bud burst, showed dark brown streaks of gummed xylem extending longitudinally through the outer vascular tissue and beyond the external margin of infection. McLarty (1933) described similar discoloration associated with artificial infections, but only occasionally recorded streaks in natural aphid-wound lesions. Production of these streaks is probably incidental to the general process of gum formation by the parenchymatous cells adjacent to the infected zone ; this response is most widespread in the young sap wood.

Since the mycelium of *G. perennans* usually spreads in the vascular tissue beyond the externally visible limits of the lesion, it is advisable, when cutting out diseased shoots, to remove 2–3 inches of the shoot below the obvious lesion to ensure that any infection in the nearby wood is eradicated.

Saprophytic phase.

During this phase the mycelium occupies all the tissues which were invaded during the parasitic phase and, in particular, the parenchymatous cells in all parts of the isolated lesion. This mycelial increase is accompanied by a progessively weaker staining reaction for cellulose. Aggregates of hyphae in the peripheral tissues give rise to acervuli, which then burst through the periderm.

In the autumn following the initiation of cankers, apothecial production may commence in the old conidial stromata of the dead bark ; formation of the perfect stage appears to be stimulated by the gradual exhaustion of the available food materials (Kienholz, 1939 ; Sharples, 1958a).

SUMMARY.

Anatomical studies on the establishment of infections by *Gloeosporium perennans* on apple branches showed that the defensive mechanism of the host comprised the production of suberized barriers by bark phellogens and the blocking of xylem vessels by gum deposition. These responses followed wounding, whether or not the wounds were inoculated with *G. perennans*, but the response was delayed by the presence of the fungus. The size and form of lesion induced by inoculation was therefore largely determined by the effect of the fungus in postponing the normal process of wound healing. This delaying effect, and consequently the invasiveness of the parasite, was greatest during the period of host dormancy.

The progress of invasion was most rapid through the sieve tubes of the phloem and the vessels and fibres of the outer xylem. Longitudinal intercellular spread through the cortex was slower. Intracellular infection of the pith and medullary ray cells occurred in pruning-wound infections. When the progress of the infection had been arrested, the phellogen and cambium laid down barriers of callus tissue consisting of parenchymatous outer cells surrounding a core of wound wood.

After the lesion had been thus isolated, the fungus remained alive as a saprophyte and subsequently formed acervuli on the exposed dead host tissue. Exceptionally, a limited spread of infection past the suberized barriers appeared to be effected through the fibre bundles of the inner cortex.

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THE INFECTION OF PRUNING WOUNDS BY *GLOEOSPORIUM PERENNANS*

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In a previous paper (1), infections resulting from the inoculation of *Gloeosporium perennans* into apple branches of two or three years of age were dealt with. It was there shown that infections could be successfully induced throughout the year by placing mycelium of the fungus in small bark wounds or spore suspension in wounds made by excising a lateral shoot. The latter gave 100 per cent. infection only in November, while 5 per cent. or less were successful in the period June–October. The rate of extension of mycelial cankers of all ages was highest between November and May, and lowest between June and October, when the wound-healing potential of the trees was at its maximum. The cankers initiated between September and April spored most heavily, the largest numbers of spores being produced during the following summer. No direct relation was established between rainfall and spore output.

The infection experiments to be described here were made on shoots less than one year old in order to study the infection of wounds of the type made during pruning. A canker induced by inoculation of the surface of a cut made just *above a bud* will be referred to as a " tip "* canker, whereas one arising from inoculation of a cut made *just below a bud* will be termed a " snag " canker. A comparison will be made of infections obtained at these two sites and of their behaviour on small shoots with that on larger branches studied in the earlier paper. The effects of the season are also considered (comparing 1955–56 with 1956–57) and the study of spore dispersal from *G. perennans* cankers is further extended.

Experimental procedure.

Snag inoculations, 1955–56.

Ten blocks of three trees in a row of dwarf pyramid Cox's Orange Pippin were inoculated as follows. In November 1955 and in March and July 1956, four first-year shoots on one tree in each block were pruned by cutting just below a bud so as to leave as long a snag as possible. Two of these snags were inoculated terminally with mycelium of *G. perennans* on an agar disc 4 mm. in diameter, and two with spore suspension at 50,000 spores per ml. The inoculum was placed on the freshly exposed surface and covered for 20 days. The length of the snag was recorded when the cover was removed and the length of the cankered portion that subsequently developed was measured at 4-monthly intervals. Gutter-type spore traps (1) were placed in position on ten of these cankered shoots one month after the inoculations were made.

In March, July and November 1956 comparable uninoculated wounds were

* This term will be used for convenience, as such a canker arises at the point where the cut is made in the routine operation of " tipping ".

made on one shoot on each of 35 trees and covered for 20 days. The shoots were randomized for position on the trees and the external length of the dead, shrunken portion of each shoot distal to the callus barrier was recorded every 4 months.

Tip and snag inoculations, 1956–57.

In November 1956 and in March, May, July and September 1957 further inoculations were made with mycelium on pruned shoots. On one tree in each of the blocks noted above, one shoot was cut just above a bud and another just below, and inoculated as before. The lengths of the resulting cankers were measured at 4-monthly intervals.

RESULTS.

Development of cankers on inoculated snags.

Owing to the variation in length of the internodes, the die-back of both infected and uninfected snags is, for comparative purposes, considered as a percentage of the length of the terminal internode left by the removal of part of the shoot.

The behaviour of the snag inoculations of the 1955–56 series is illustrated in Fig. 1. The inoculations made with mycelium in November 1955 and March 1956

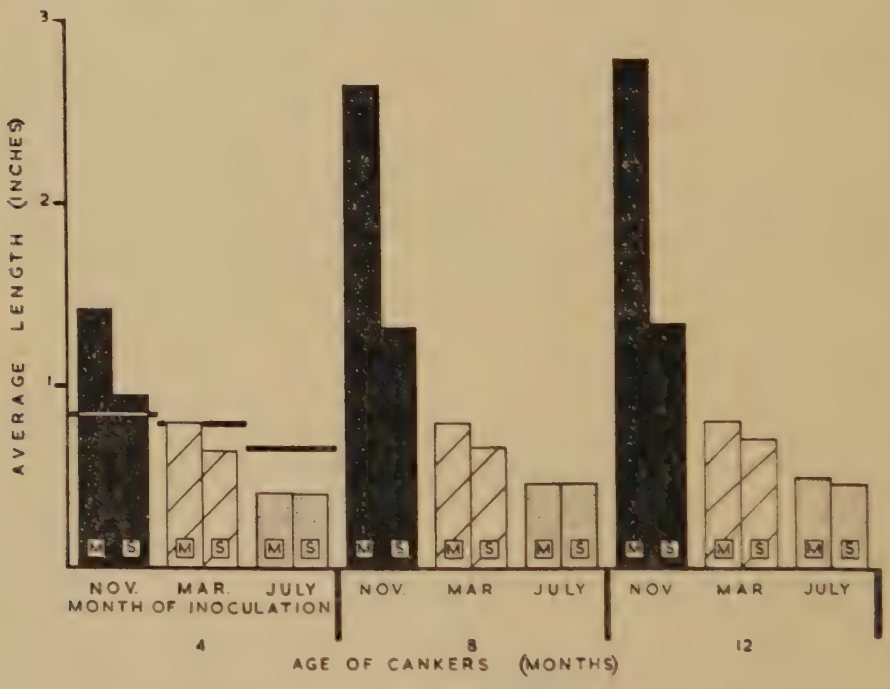

FIG. 1.

Average length of snag cankers of *G. perennans* at intervals of 4 months. The average length of the terminal internode is shown as a horizontal line against the length of the cankers after 4 months. M, mycelial inoculations; S, spore inoculations.

resulted in longer cankers than those made with spores, but the July 1956 inoculations, whether made with spores or mycelium, resulted in cankers of equal length. The suggestion has already been made (Corke, 1) that inoculation with mycelium confers an initial advantage over inoculation with spores ; these results support this supposition, except when the host is growing vigorously in the summer and is able to react as effectively against established mycelium as against freshly germinated spores.

The November inoculations with mycelium induced snag cankers which, after 4 months, were more than fifteen times as long as the die-back on uninfected pruning snags made at the same time of year. In the July series, however, the average length of the inoculated snags after the same time was only 0·4 in., compared with 0·2 in. for the control, uninfected snags. The size attained by these July-initiated cankers thus appears to have been due as much to the natural process of dying back as to the presence of *G. perennans*.

Although the average length of the snag cankers from the November inoculations exceeded that of the terminal internode after the first 4 months, one mycelial canker and eleven cankers from spore suspension failed to extend beyond the first living bud. After 8 months, however, all the November-inoculated mycelial cankers and all but one of the spore-suspension cankers of this series had spread beyond the first bud (Table I). The March inoculations resulted in cankers of intermediate size, of which only about one-third of the mycelial and none of the spore-suspension ones extended past the bud. It is worthy of note that five of the July mycelial cankers extended as far as the bud, while one from spores showed slight activity during the winter months, although this may have been infected at a later date. Very little increase in length took place after July in any of the November or March cankers and, as has already been shown, the July cankers all remained small.

Die-back of uninfected pruning snags.

The rate at which uninfected snags died back during the first 4 months was twice as fast after pruning in March 1956 as when pruned in July and five times as fast as when pruned in November (Table II). Very little die-back occurred between November 1956 and March 1957 but, whereas the snags made in the previous March died back only a further 3 per cent. in the period March–July 1957, those made in July and November died back an additional 20 per cent. and 40 per cent. respectively.

Following the removal of part of a shoot, the extension growth arising from the lateral bud situated just below the cut would be expected to be more vigorous after pruning in March than in July, while no growth would result for some months after pruning in November. In this instance the growth of shoots in 1956 from the base of snags made in November 1955 was much less vigorous than that in 1957 from snags made in November 1956, while only one shoot developed after pruning in July. These results suggest that the degree to which the snags died back was influenced not only by the time at which the shoots were cut in relation to the period of active growth, but possibly also by the growth which developed from the bud at the base of the snag, even where this was delayed until the succeeding year.

Comparison of tip and snag cankers.

In the tip inoculations of the 1956–57 series of experiments, the most rapid increase in length of the infected area took place during the first 4 months after

Table I.

Extension of snag cankers (1955–56 series).

Month of inoculation	Inoculum	Age of canker (months)	Average length of canker (inches)	Average length of terminal internode (inches)	Average length of canker (% of terminal internode)	Percentage of shoots dead beyond first bud
November 1955 ..	Mycelium	4 (Mar. 1956)	1·42	0·85	>100	94·4*
		8 (July 1956)	2·64			100
		12 (Nov. 1956)	2·79			100
	Spores	4	0·94	0·86	>100	38·9*
		8	1·32			94·4
		12	1·34			94·4
March 1956	Mycelium	4 (July 1956)	0·79	0·77	>100	30
		8 (Nov. 1956)	0·79			30
		12 (Mar. 1957)	0·81			30
	Spores	4	0·65	0·85	76·3	0
		8	0·67		78·8	0
		12	0·70		82·2	0
July 1956	Mycelium	4 (Nov. 1956)	0·41	0·65	63·0	0
		8 (Mar. 1957)	0·45		69·1	0
		12 (July 1957)	0·50		76·9	0
	Spores	4	0·41	0·70	58·5	0
		8	0·46		65·8	5
		12	0·46		65·8	5

* One tree was removed after inoculation, with loss of 2 spore-suspension and 2 mycelial inoculations.

TABLE II.

Die-back of uninfected snags (1956 series).

Month of pruning	Age (months)	Average length of dead portion (inches)	Average length of terminal internode (inches)	Average length of dead portion (% of terminal internode)
March 1956 ..	4 (July 1956)	0·48	0·80	60·0
	8 (Nov. 1956)	0·53		66·3
	12 (Mar. 1957)	0·58		72·5
	16 (July 1957)	0·61		76·3
	20 (Nov. 1957)	0·63		78·7
July 1956 ..	4 (Nov. 1956)	0·20	0·55	36·4
	8 (Mar. 1957)	0·22		40·0
	12 (July 1957)	0·35		63·6
	16 (Nov. 1957)	0·35		63·6
November 1956	4 (Mar. 1957)	0·09	0·91	9·9
	8 (July 1957)	0·49		53·9
	12 (Nov. 1957)	0·54		59·3

inoculation in November. Extensive die-back and the death of the first bud followed all tip inoculations except those made in March, only half of which killed the bud (Table III). Fewer buds were killed as a result of the snag inoculations ; no buds died on March-inoculated snags, while only on those inoculated in May and September were they all killed.

A comparison of the rates of extension of tip and snag cankers shows no great difference between those made in September and November, even though host reaction to fungal penetration is at a low level in the latter month. Cankers initiated in March, May and July, however, showed considerable variation, though host reaction might be expected to be fairly constant over these months. As in the previous series of inoculations, only limited increases in length occurred after July, with the exception of tip cankers initiated in July and both tip and snag cankers initiated in September.

The behaviour of the March cankers may be attributed to the healing which took place when growth began, enabling half the buds immediately below the tip cankers to survive. Although the July cankers increased in length at about the same rate as the March ones, indicating that there was little change in host reaction, the shorter internodes in July resulted in the loss of half the buds at the base of snags, and all those immediately below tip cankers. After the death of the first bud these cankers became, in effect, snag cankers and they increased in length during the following winter in the same way as those initiated in September and November.

The similarity between the rates of extension of May tip and snag cankers was again due to the loss of all the first buds, the tip cankers thus becoming snag cankers. The large size attained by them was probably the result of conditions which are discussed more fully later.

Seasonal effects.

Four months after inoculation, the length of snag cankers induced in November 1955 was twice that of those induced in November 1956 and, although the internodes

TABLE III.

Comparison of tip and snag cankers in relation to length of terminal internode (1956–57 series).

Month of inoculation	Type of wound inoculated	Age of canker (months)	Average length of canker (inches)	Average length of terminal internode (inches)	Average length of canker (% of terminal internode)	Percentage of shoots dead beyond first bud
November 1956 ..	Tip	4 (Mar. 1957)	0·74	0·14	>100	100
		8 (July 1957)	0·79			100
		12 (Nov. 1957)	0·82			100
	Snag	4	0·68	0·71	95·8	30
		8	0·76		>100	30
		12	0·76			30
March 1957	Tip	4 (July 1957)	0·22	0·11	>100	40
		8 (Nov. 1957)	0·23			50
		12 (Mar. 1958)	0·33			50
	Snag	4	0·47	0·70	67·0	0
		8	0·49		70·0	0
		12	0·49		70·0	0
May 1957	Tip	6 (Nov. 1957)	0·62	0·09	>100	90
		8 (Jan. 1958)	0·63			100
		12 (May 1958)	0·63			100
	Snag	6	0·65	0·36	>100	100
		8	0·66			100
		12	0·68			100
July 1957	Tip	4 (Nov. 1957)	0·49	0·08	>100	100
		8 (Mar. 1958)	0·87			—
	Snag	4	0·42	0·39	>100	50
		8	0·42			—
September 1957 ..	Tip	4 (Jan. 1958)	0·56	0·12	>100	100
		8 (May 1958)	1·73			100
	Snag	4	0·70	0·49	>100	80
		8	1·53			100

were longer in 1955, 89 per cent. of the inoculated shoots died beyond the first bud in 1955–56 compared with 30 per cent. in 1956–57. On the first occasion, inoculations were made after 4 months of dry weather with above-average temperatures and were followed by a dry spring ; in 1956, 3 of the 4 previous months were wet and the following months were unusually wet and warm. It may be mentioned here that, judged by the previous ten years in each case, flowering of Cox was a week late in 1956 and 2 weeks early in 1957. It seems probable that in the warm, wet early months of 1957 there may have been more water in the tissues than is normal at this time, with consequent effects on host/parasite relations.

Similar results were obtained from snag inoculations made in March : cankers of 1956 were almost twice as long as those of 1957 and, whereas 30 per cent. of the buds died in 1956, none was killed in the following year when growth was more vigorous. As the weather following these inoculations was fairly dry in both years, the condition of the tissues at the time of inoculation may be a more important factor than that in the ensuing period. The results of the July snag inoculations support this hypothesis, since no buds were killed in 1956, while 50 per cent. died in 1957, in which year June was drier and warmer and the internodes were much shorter. In both years April and May were drier than usual, and it was in May 1957 that all the buds were killed following inoculation of both snags and tips. Because of the proximity of the bud to the cut surface on a normally pruned shoot, the effects of drought were most readily observed on the tip cankers. March tip cankers were the smallest of all and fewest buds were killed as a result of inoculation ; as mentioned above, the trees were unusually forward at this time. Like the May tip inoculations, those made in July resulted in the death of all the buds immediately below.

Spore production by snag cankers.

Gutter-type spore traps were placed beneath ten active snag cankers a month after they had been initiated by inoculation with *G. perennans*. Spores were recorded on the November-initiated cankers in December 1955, and these cankers gave more than 100,000 spores each month until August 1957, with the exceptions of February 1956 and April 1957.

The March 1956 cankers also began to produce spores after a month, but the numbers remained below 100,000 until July ; during the next 12 months an average of about 200,000 spores per month was caught. The first spores from the July 1956 cankers were observed in December, but only in January and July 1957 did the number exceed 100,000.

The total numbers of spores collected monthly between mid-December 1955 and the end of December 1957 from each series of cankers are shown in Table IV. The loss of one collection in September and two in December 1956, due to high winds and frosts respectively, resulted in reduced numbers.

Since the number of spores collected from both the November and March cankers was greatest in July 1956, this must have been about the time of maximum spore production for all cankers resulting from infections during the previous winter. Conditions were again suitable for sporulation during the relatively warm, wet months of December 1956 and January 1957, and again in the period May–July 1957. At this time the output of the March and July cankers increased slowly while that of the November cankers decreased.

Table IV.

Total number (thousands) of spores collected each month from ten cankers.

Month of collection		Month of inoculation		
		November 1955	March 1956	July 1956
1955	December ..	258		
1956	January ..	618		
	February ..	60		
	March	835		
	April	1,313	15	
	May	120	20	
	June	4,374	85	
	July	21,688	2,892	
	August	3,120	380	
	September ..	2,395	126	
	October	1,495	230	
	November ..	1,460	43	
	December ..	7,010	73	10
	Total ..	44,488	3,864	10
1957	January ..	8,810	158	108
	February ..	560	103	27·5
	March	455	325	20
	April	0	0	0
	May	2,050	58	30
	June	2,297	100	45
	July	995	345	468
	August	0	0	0
	September ..	15	10	2·5
	October	205	25	0
	November ..	70	185	0
	December ..	215	33	0
	Total ..	15,672	1,342	701

DISCUSSION.

The results given in the earlier paper (1), dealing with branch cankers resulting from inoculations with mycelium and spores made monthly throughout the year, are not entirely comparable with those given above, since the shoot inoculations were made every 4 months from November 1955 until March 1957 and thereafter every 2 months until September 1957. However, a comparison of the lengths of branch cankers induced by inoculation with mycelium in November, March and July (1953–54) with those of shoot cankers initiated with mycelium in the corresponding months of 1955–56 shows that the relative effects of the month of inoculation were the same in the two series : cankers initiated in November extended farthest, while those made in July were the smallest.

In comparing cankers induced by spore inoculations in the two series, it is seen that the November and March results on shoots were similar to those on branches but that, whereas July inoculations were unsuccessful on branches, short cankers equal in length to those from mycelium were induced on shoots.

The degree of correspondence between the results on shoots and the earlier findings on branches is closer than might have been expected. On the branches, the inoculations with mycelium were made laterally through wounds in the bark, while the spores were placed on the surface exposed by removing a side-shoot. On the shoots, all the inoculations were made on the surface of a terminal cut, and the course of development was influenced by the natural process of dying back from the cut.

Where the pruning cut was made below a bud in order to leave a long snag, the rate at which the snag died back varied according to the time of year. Thus, pruning snags made in March died back twice as fast in the ensuing 4 months as those of July and five times as fast as those of November. With the exception of those of November, at which time there is no active host reaction to such wounding, inoculated snags died 0·2–0·3 in. farther than the uninfected control snags in the same time. This suggests that host resistance to further penetration by *G. perennans* remained approximately the same during the period March–October, so that the total die-back of the March snags was twice that of July snags, whether they were infected or not. It has already been suggested that the die-back of uninfected snags may also be influenced by the growth which develops from the apical bud. This bud is left to perform the functions of the terminal bud which has been removed, and Wray (4) found that the changes which occurred were mainly controlled by the amounts of food and water available ; also that the demands of an active bud were met, in part, by the transfer of food and water from a snag, if present. This may explain the differences in the die-back of uninfected snags in the current season, and also the death of a further 20 per cent. and 40 per cent. respectively of the July and November snags during the ensuing summer, when growth took place from the adjacent buds. Similar results were not obtained with the snag cankers, since the length of most of these was 60 per cent. of the length of the terminal internode after the first 4 months.

When the pruning cut was made immediately above a bud the snag was reduced to a minimum, and during the summer this frequently dried out beyond the bud left at the end of the shoot (Fig. 2). Observations on Cox shoots summer-pruned in 1957 showed that, by December, 23 per cent. of the buds had died, and that some shoots were dead to 1·25 in. from the tip ; a further 25–30 per cent. died before growth was resumed in 1958.

Observations on uninfected snags, and on snag cankers which had not killed the bud, showed that a final callus formed near the base of the snag when the die-back had reached a point not less than 0·15 in. above the bud (Table II). This would appear to be an almost ideal point at which to cut a shoot so that, while preserving the bud by assisting the successful sealing of the exposed tissues, it leaves the minimum amount of tissue which would be expected to become available for fungal attack. A length of about 0·25 in. is suggested as the amount that would normally be sufficient to buffer the effects of water loss due to summer pruning, although in dry seasons this length might prove insufficient ; in 1957, for example, snags of more than 0·4 in. in length dried out so fast that the subtending buds were killed.

Detailed records have already been given (Corke, 1) of the numbers of spores collected during the period May–November 1955 from selected branch cankers initiated between September 1953 and February 1954. In that year the highest number of spores was recorded in September and the November record was approximately the same as that of June. Subsequent records taken until the end of December 1957 show that

in 1956 there was a peak in spore production in June–August, with a minor one in December–February 1957 and a final small one in May 1957.

The importance of snag cankers as sources of spores has been shown by Guthrie (2), and in the present series of records (Table IV) the November-induced cankers were found to give 91 per cent. of all the spores collected, as against 8 and 1 per cent. for those induced in March and July respectively. The pattern of spore production also showed a close similarity to that of the branch cankers, with a peak in July 1956, a smaller peak in December–January 1957 and another in May–July 1957. Thus, the records of spore output in both series show that the winter-initiated cankers were the most productive and that there was a peak of spore production in the summer, while the rise in numbers produced in the period December 1956–February 1957 probably reflected the unusually mild weather of that date.

While the 1956–57 records corroborated those given in the earlier paper in showing that there was no direct correlation between rainfall and the number of spores disseminated, the influence of rainfall in causing fluctuations in spore production during the summer has been made clearer. Since the spores require rain for dispersal, low rainfall exerts some control over the numbers of spores collected. In 1955, rainfall was very low until November, and only thereafter did the numbers collected show any real decrease ; in 1956, on the other hand, rainfall was considerable in the period June–August, so that all the spores produced were probably washed off each month. It seems likely, therefore, that the peak reached in September 1955 was mainly due to an accumulation, through lack of rain, of spores produced during the preceding months.

Summarizing the main points relating to wood infections arising from the work on both branch and shoot infections, it is clear that the size of lesions depends on the wound-healing activity of the host, which is at its maximum during the summer. This renders branch wounds virtually non-susceptible to infection during the summer, but wounds made by tip pruning are never entirely resistant because of the rapid loss of water from the tissues, which leads to the formation of dead snags of various lengths in which the vessels are frequently unable to become completely sealed (4). In addition, a number of workers have shown that fungal spores may be actively sucked into the vessels of shoots cut during the summer. Since the callus normally formed in a snag is about 0·2 in. above the subtending bud, it is suggested that, if summer pruning is done, at least an internode might be left temporarily to act as a buffer between the bud required for further growth and the effects of climatic conditions which may cause its death. An infection of such a snag would result in a much smaller lesion than would be formed if the bud died. The importance of size rests on the contribution made by these infections to the spore load on the tree prior to their removal during winter pruning. Table IV suggests that sporulation normally decreases rapidly in late summer and it has already been noted that the contribution of summer-initiated cankers to the total spore load is very small.

Winter-pruning wounds, on both shoots and branches, are very susceptible to *Gloeosporium* infection and, unless carried out in cold, dry weather, such pruning may encourage the establishment of lesions which extend rapidly and make the largest contribution to the spores present in the summer. Because of this, it would be an advantage, where summer-pruning wounds have become infected, to remove as much dead material as possible without injuring the callus. The later that winter pruning is done, the smaller will be the chance of large lesions resulting, while the

PLATE I

FIG. 2.

Tip of shoot of Cox's Orange Pippin showing buds almost isolated by die-back 4 months after pruning on 12th August 1957.

[*face p.* 94

thorough removal of all obvious cankers at this time has been shown by Hamer (3) to be of practical value in reducing the level of inoculum on the tree.

SUMMARY.

Inoculations of pruning wounds on apple shoots with *Gloeosporium perennans* showed that, unlike branch wounds, the cut tips of shoots were more or less susceptible to infection with spores throughout the year and that, although the extent of the infection was subject to the same host reactions as operated on lateral branch cankers, the normal healing process might be affected by seasonal conditions. This was shown by comparing the behaviour of infected pruning cuts made on shoots at comparable times in successive years.

Spore production from infected shoots was found to be greater from November than from March infections and to begin in both instances after one month ; July-initiated infections first spored in December and produced very few spores. Like the branch infections studied in 1953–54, the shoot cankers gave considerable numbers of spores in the warm, wet months of December 1956–February 1957. The peak spore collection from the shoot cankers was in the June and July following inoculation and this was also a peak period for sporulation on the branch cankers.

ACKNOWLEDGMENTS.

The author wishes to thank Miss M. Marlow and Miss M. Waller for their assistance in carrying out the inoculations and recording the results. The meteorological records were taken by Mr. G. E. Clothier and the photograph by Mr. D. E. Aliband.

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OBSERVATIONS ON THE GROWTH OF THE FRUIT ON GLASSHOUSE TOMATO PLANTS BETWEEN MARCH AND SEPTEMBER

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THE general growth trends of the main organs of the tomato plant in heated glasshouses—roots, shoots, leaves and fruits—were discussed in an introductory paper (Cooper, 1958). The present paper deals in more detail with the growth of the fruits from March to September.

Technique.

Observations were made on three single-stemmed plants of the variety Potentate grown in a glasshouse border during each of the years 1954–56 ; in the first year at the Cheshunt Experimental Station in the Lea Valley and after that at the Glasshouse Crops Research Institute in the Worthing area. It was not possible to use more than three plants, as much labour was needed to record and analyse the data. Axillary shoots which developed on the main stem were removed as soon as they appeared. No leaf was removed until the major part of the lamina had lost its green colour and was largely dry and brown. Measurements were made at weekly intervals of the diameters of the fruits. Fruits were not removed until fully ripe. Cultural details are given in the introductory paper referred to above.

The seed was sown on 13th January 1954, 21st December 1954 and 22nd November 1955.

Method of estimating fruit volume.

The mean diameter of each fruit was determined by measuring it equatorially, in two directions at right angles, with sliding vernier calipers. Where a fruit was obviously not symmetrical the measurements recorded were those of the greatest and least diameters. From the cube of the mean radius the volume of each fruit was calculated. In this way an estimate of the total volume of fruit on the plants was obtained at weekly intervals without damage to the plants.

To test the accuracy of the method the true volumes of one hundred green fruits ranging in size from 3 ml. to 230 ml. were determined by displacement. The mean diameters were obtained as described, and the estimated volumes were calculated from them. The correlation coefficient between the estimated and the true volume was +0·996. Because the tomato fruit is a flattened sphere the estimated volume was always greater than the true volume. The mean percentage over-estimation for the one hundred fruits was 23 per cent. The degree of over-estimation was found to be independent of the size of the fruit since there was no significant correlation between the percentage over-estimation and the size of the fruit.

Results.

Relationship between the number of fruits appearing and (a) time of year, (b) age of plant.

In Fig. 1 the moving averages, based on three consecutive weekly observations, of the number of fruits appearing per plant are shown plotted against the time of initiation of the fruits, assessed as petal fall. Moving averages have been used to reduce the obscuring effect of short-term fluctuations in growth rate on the general trends. The data show that in all three years the number of fruits appearing each week rose sharply to a high level and then gradually declined. The decline from the high rate began on approximately 18th, 17th and 22nd May in 1954, 1955 and 1956 respectively, despite the widely differing dates on which fruit first began to appear and the different lengths of time over which the high rate was maintained.

Fig. 2, showing these same data plotted against the age of the plant at the time of appearance of the fruit, demonstrates that the high rate of appearance of fruit was first attained each year when the mean ages of the plants from sowing were 126, 134 and 134 days in 1954, 1955 and 1956 respectively.

In the environment of a commercial glasshouse, and with the cultural practices employed, the high rate of fruit appearance is first attained when the plant reaches an age of approximately 130 days from sowing (Fig. 2), and this rate is maintained until approximately the third week in May (Fig. 1). The length of time over which the high rate is maintained is greater the longer the time interval between the date of sowing and the third week in May, viz. approximately 125, 145 and 175 days in 1954, 1955 and 1956 respectively.

Relationship between maturation period of fruits and (a) age of plant, (b) time of year.

In Fig. 3 the mean lengths of the maturation periods (i.e. the time interval between petal fall and picking) of the fruits appearing each week are plotted against the ages of the plants, in days from sowing, at the time of appearance of the respective fruits. For most of the growing season the fruits had a maturation period of approximately 60–70 days. During a relatively short part of it, however, the maturation period lengthened considerably. In all three years, fruits appearing when the plants were about 160 days from sowing had the longest maturation period, despite the different sowing dates and the differing dates on which fruits first began to appear.

When the maturation periods of fruits are considered in relation to the dates at which they appeared, there is no evidence of any relationship between the lengthening of the maturation period noted above and the time of the year, since the fruits with the longest maturation period appeared in mid-June, late May and late April in 1954, 1955 and 1956 respectively.

Relationship between growth curves of fruits and (a) age of plant, (b) time of year.

It was noticed that some fruits increased rapidly in size soon after appearing, while others increased slowly at first and later more rapidly. To obtain a simple quantitative measure of this phenomenon the cube of the radius, determined half-way through the maturation period, was expressed as a percentage of the cube of the radius of the mature fruit, thus giving the " half-period " value. Thus if the percentage obtained were less than 50, more growth occurred in the second half of the maturation period than in the first.

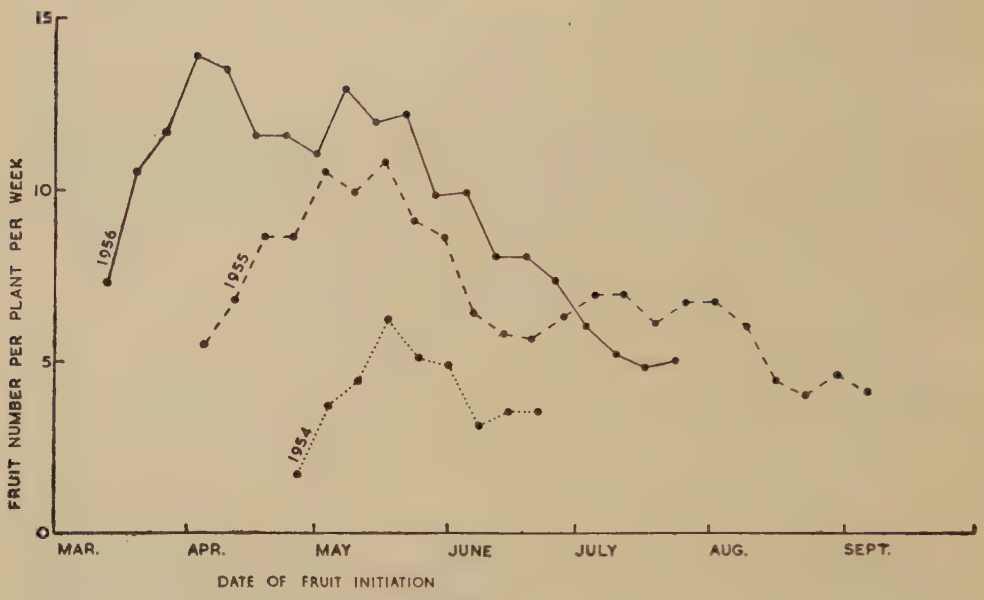

Fig. 1.

Rate of appearance of tomato fruits in relation to time of year.

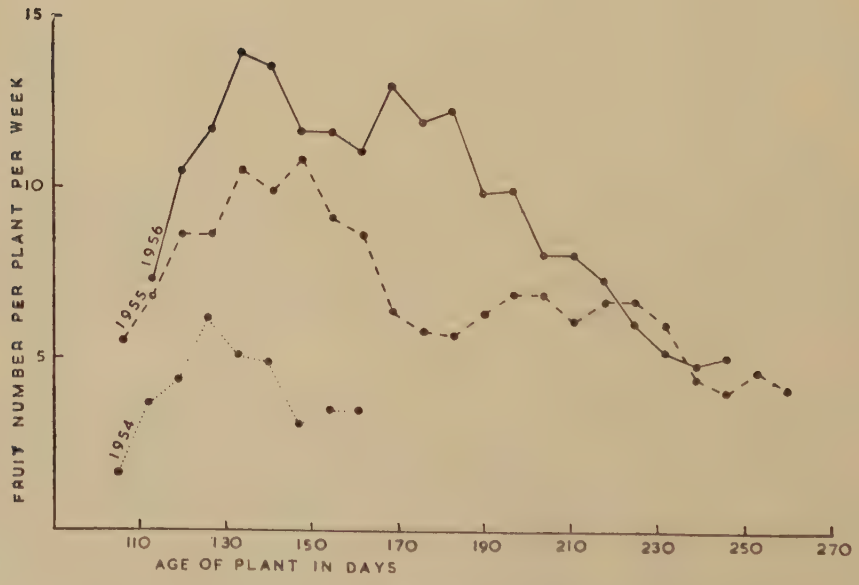

Fig. 2.

Rate of appearance of tomato fruits in relation to age of plant.

When the data so obtained were plotted against the date of appearance of the fruits there was no evidence of any effect of the time of the year on the initial growth lag.

In Fig. 4 the mean half-period values of the fruits appearing each week have been plotted against the age of the plant in days from sowing. In 1954 and 1955 the greatest initial lag in fruit growth, when only one-fifth of the total growth was made in the first half of the maturation period, occurred at approximately the same number of days from sowing, thus suggesting that there might be an effect of the age of the plant. But in 1956 there was no marked departure from fairly steady growth of the fruits at any age of the plant.

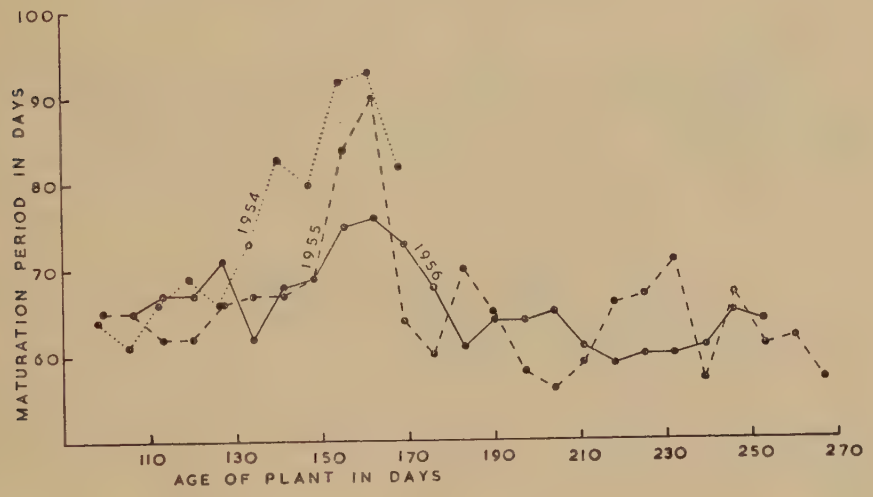

Fig. 3.

Length of maturation period of tomato fruits in relation to age of plant.

In Fig. 5 the mean half-period values per truss are shown in relation to truss position as numbered from the base of the plants upwards. In all three years there was a departure from steady growth and this was associated with truss position, the greatest initial lag occurring in the 6th, 7th and 8th trusses in 1954, 1955 and 1956 respectively. In these trusses only 34, 23 and 38 per cent. of the total growth of the fruit was made in the first half of the maturation period, i.e. truss position, independent of time of year or age of plant, may affect the growth-rate pattern of the fruits.

Relationship between fruit size at maturity, maturation period and the form of the growth curve.

Table I shows the partial correlation coefficients for the mature size of the fruits, the duration of the maturation period and the form of the growth curves of the fruits (expressed as the percentage of the total growth made during the first half of the maturation period).

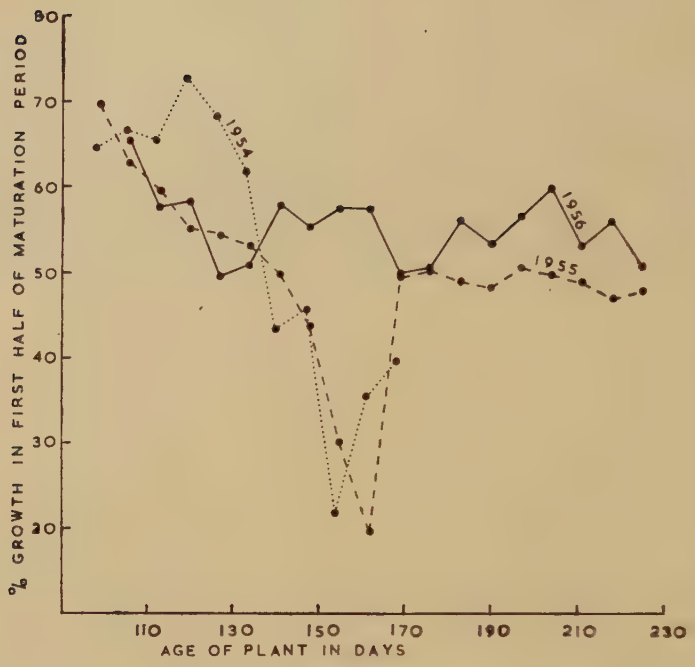

FIG. 4.

Initial lag in growth of tomato fruits in relation to age of plant.

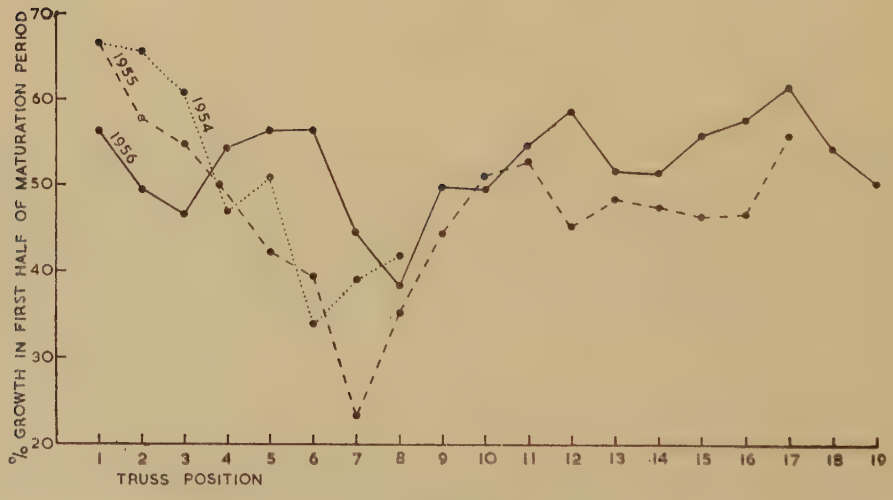

FIG. 5.

Initial lag in growth of tomato fruits in relation to truss position (numbered from the base of the plant upwards).

TABLE I.

Relation between fruit size, maturation period and form of growth curve.

Partial correlation	1954	1955	1956
Fruit size and maturation period ..	−0·37**	−0·05 n.s.	−0·12*
Fruit size and form of growth curve ..	−0·06 n.s.	+0·13*	+0·28**
Form of growth curve and maturation period	−0·75**	−0·68**	−0·59**

n.s., non-significant ; * P=0·05 ; ** P=0·01.

The only partial correlation that was consistently highly significant ($P=0·01$) in all three years was that between the duration of the maturation period and the form of the growth curve. This implies that fruits that develop slowly initially have a longer maturation period than fruits that develop more rapidly initially. The sizes of the mature fruits, however, were not consistently correlated with either the length of the maturation period or the form of the growth curve.

Relationship between fruit position within the truss and fruit growth.

Corbett (1925) stated that " when a truss bears a large number of fruits there is a considerable lengthening of the maturation period of those after the seventh, eighth or ninth ". He later (1926) stated that the maturation periods " of all the fruits of the first truss and the first seven or eight fruits of all the other trusses were reasonably constant, but the later fruits of the second, third and fourth trusses took longer to ripen and, therefore, there was a sudden increase in the maturation period ". He further stated (1927) that " in the fruits of the second, third, fourth and fifth trusses the maturation period of successive fruits on the same truss lengthens ". There is some conflict between these statements, especially as regards the maturation period of successive fruits in trusses other than the first. It should be noted, however, that the data presented in 1925 and 1926 were obtained from the varieties Ailsa Craig, Comet and Manx Marvel, whereas in 1927 a different variety, E.S.1, was used.

Beadle (1937), working with Kondine Red and considering the first six fruits in the trusses, found that the fruits had a shorter maturation period the nearer they were to the main stem. Kidson and Stanton (1953) obtained a similar result with the variety Potentate. Kerr (1955), working with the variety Farthest North and considering the first six fruits in each truss, stated that there was a significant difference in the number of days to maturity, fruits at the distal end taking longer to mature.

The mean maturation period for each of the basal seven fruits in all trusses in the present experiments is adequately represented by a linear regression relating maturation period in days (M) and fruit position in the truss (P) (the order being from proximal to distal), as follows :

$$1954,\ M = 69·1 + 2·0P$$
$$1955,\ M = 57·7 + 2·5P$$
$$1956,\ M = 63·6 + 0·8P.$$

All three regressions are significant and imply that the maturation period is longer the more distal the fruit position within the truss. This is in agreement with the findings of all the workers referred to above with the exception of the 1925 and 1926 reports of Corbett.

Beadle (1937) also reported that the nearer a fruit was to the main stem the larger the size it attained. The data for 1954 on mean mature fruit volumes for each fruit position within the truss and for all trusses are in agreement with the findings of Beadle. There was a significant linear regression relating mature fruit volume (V) and fruit position in the truss (P), the order being from proximal to distal :

$$V = 19{\cdot}6 - 1{\cdot}3P.$$

In 1955 and 1956, however, there was no significant difference between the mean sizes of the first seven fruits in the trusses.

The third aspect of fruit growth considered—the form of the growth curve—was significantly related to fruit position within the truss in both 1954 and 1955, the more distal the fruit the smaller the percentage of growth made in the first half of the maturation period. There were in both years significant linear regressions relating the half-period value (H) and fruit position in the truss (P) :

$$1954,\ H = 62{\cdot}4 - 2{\cdot}9P$$
$$1955,\ H = 52{\cdot}9 - 1{\cdot}4P,$$

but in 1956 there was no relationship with fruit position, just over 50 per cent. of the total growth being made in the first half of the maturation period irrespective of fruit position.

It can thus be concluded that in all three years there was a relationship between the position of a fruit in a truss and the length of its maturation period. In one year there was an apparent relationship between fruit position and mature fruit size, but in the other two years this relationship was not found. In two years out of three there was a relationship between the position of a fruit in a truss and the form of its growth curve.

SUMMARY.

1. A non-damaging method of estimating the volume of a tomato fruit while still attached to the plant is described and its accuracy assessed.

2. Evidence is presented suggesting that there is a relationship between the rate of appearance of fruits in the Potentate variety of tomato and both the time of the year and the age of the plant.

3. A relationship is demonstrated between the length of the maturation period of a fruit and the age of the plant.

4. Possible effects of plant age and truss position on the forms of the growth curves of fruits are discussed.

5. It is shown that fruits that begin to swell rapidly on appearance have a shorter maturation period than those fruits that have a period of initial lag before rapid growth begins.

6. The relationships between fruit position within the truss and fruit growth are discussed, and it is shown that the more distal the position of a fruit the longer is its maturation period.

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OBSERVATIONS ON THE GROWTH OF THE LEAVES OF GLASSHOUSE TOMATO PLANTS BETWEEN MARCH AND AUGUST

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The development of the tomato plant in a heated glasshouse throughout the growing season was discussed in a previous paper (Cooper, 1958). The present paper deals in detail with the growth of tomato leaves during the same period of time.

Technique.

Three plants of the variety Potentate were grown in a glasshouse border during 1955 and 1956. It was not possible to use more than three plants as much labour was needed to record and analyse the data. The seed was sown on 21st December 1954 and 22nd November 1955. The plants were grown 6 ft. apart to reduce competition. No leaf was removed until the major part of the lamina had lost its green colour and was largely dry and brown. Measurements were made at weekly intervals of the length of the leaves from the axil to the tip. Axillary shoots developing on the main stems were removed as soon as they appeared.

Method of estimating leaf area.

Lyon (1948) working with the Bonny Best variety stated that there was " a simple mathematical relationship between the overall length of the leaf and the total area of the leaflets. The form of the leaf seems to remain essentially constant, regardless of its size." The relationship deduced was that leaf area equalled 0·1551 multiplied by the square of leaf length. Porter (1937) reported a relationship, for the Grand Rapids Forcing variety, between leaf area and length of the leaf from the base of the first leaflets to the tip of the midrib. This relationship was :

$$\text{leaf area} = 3{\cdot}16 + 0{\cdot}417x + 0{\cdot}307x^2,$$

where x = leaf length.

During 1955 and 1956 forty-one leaves at varying stages of maturity and ranging in length from 4·1 cm. to 52·1 cm. were removed from adjacent non-experimental plants of Potentate at different stages of development of the plants and from different positions. The outline of each leaf was marked on paper, the area determined with a planimeter, and the length from the axil to the tip was measured. The data relating leaf length to leaf area were found to lie on a straight line when plotted on a logarithmic scale for both length and area, the equation of the line being :

$$Y = 0{\cdot}799 + 2{\cdot}3363X,$$

where Y = log. leaf area and X = log. leaf length. The use of this equation provided a rapid method of estimating area without damage to the plant.

Results.

Development of the leaves.

The number of leaves appearing each week did not vary systematically between March and August, the criterion of leaf appearance being the attainment of a length of 0·5 cm. The calculated line of closest fit to the 1956 data was horizontal, the mean weekly rate of appearance being 2·6 leaves. In 1955, although there were pronounced short-term fluctuations, the calculated line of closest fit to the data was a first order polynomial, but the mean weekly rate of appearance of leaves only changed from 2·1 in early March to 3·0 by early September. Similarly, there was no apparent effect of the time of year between March and August on the senescence of leaves, the mean weekly rate being 0·7 in both years.

In Fig. 1 are shown, plotted according to date of appearance, the mean growth periods (time in days from appearance to attainment of maximal length) for leaves appearing from March to July. In both years the growth period steadily decreased until a minimum was reached in late May or early June, after which the duration of the growth period increased. Leaves appearing in late May or early June attained their final size in approximately 32 and 27 days in 1955 and 1956 respectively, as against 48 and 44 days in early March and 38 and 35 days in mid-July. The data thus suggest a relationship between the time of the year at which a leaf appeared and the number of days of growth before it attained its final size.

The form of the growth curve of individual leaves was also related to the time of year at which they appeared. To obtain a simple estimate of the form of the growth curve the length of the leaf half-way through the growth period (the half-period value) was expressed as a percentage of the length of the mature leaf. Thus, if the percentage were less than 50, more growth occurred in the second half of the growth period than in the first, and conversely if it were greater.

In Fig. 2 the mean half-period values for the leaves appearing each week are plotted against the dates of appearance. In 1956 the calculated curve of closest fit declined to a minimal value for leaves appearing in early June and then rose again. For the 1955 data the mean value for the whole period has been inserted. It is of interest to note that in 1955 *all* the half-period values during late April to late June were below this mean. Thus in both years from late April to late June the half-period values were low and minimal values were reached.

In Fig. 3 the mean mature lengths of leaves appearing from March to July are plotted against date of appearance of the leaves, and in Fig. 4 against age of the plant at the time of appearance of the leaves. As shown by the calculated lines of closest fit, mature leaf size decreased in both years as age of the plant increased, but it also decreased as the date of appearance of the leaves progressed from March to July. The time span covered is thus too short to determine whether the true relationship is with plant age or with date of appearance.

There was no evidence of any relationship between the age of the plant (over the age range of 71 to 288 days from sowing) and the rate of appearance of leaves.

Similarly there was no indication of a consistent relationship between the age of the plant and the duration of the growth periods of the leaves ; nor of any relationship between the age of the plant at the time of appearance of a leaf and the form of the growth curve of that leaf.

There was also no evidence of a consistent relationship between age of the plant

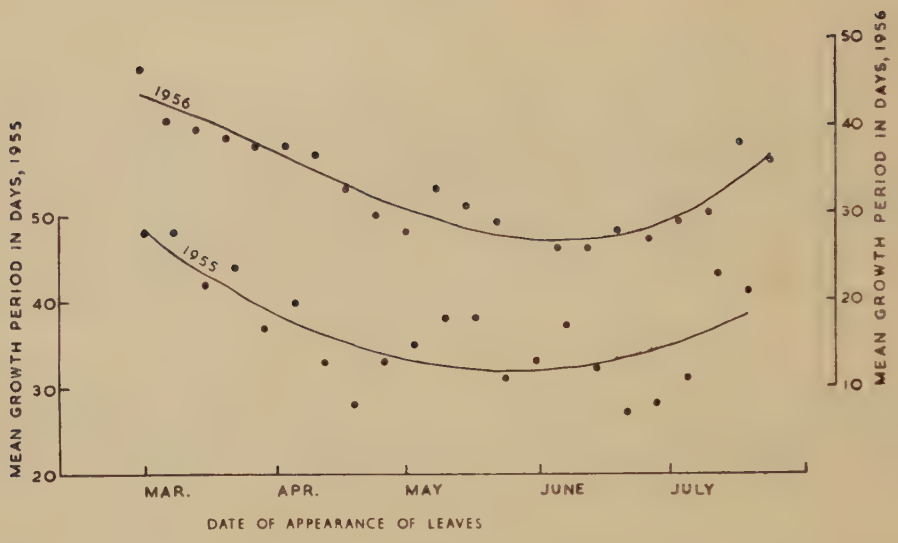

FIG. 1.
Growth period of tomato leaves in relation to date of their appearance.

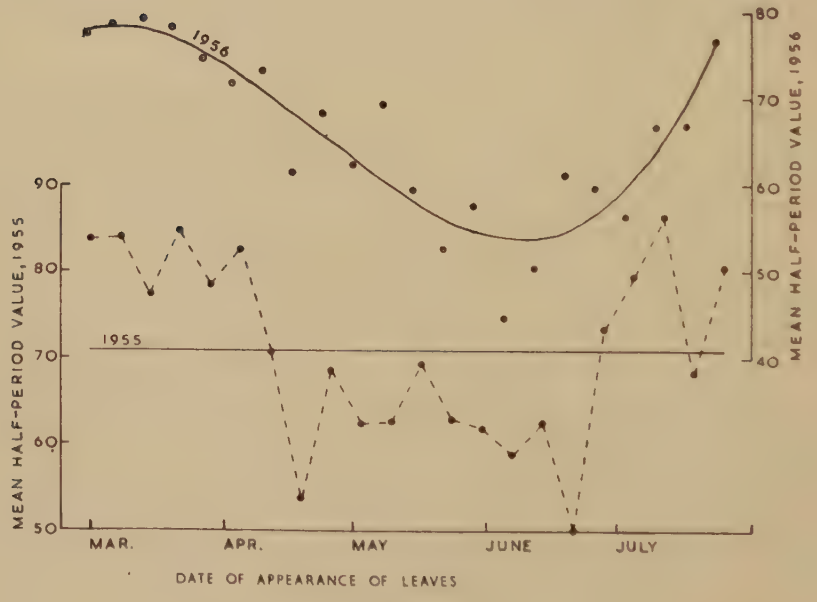

FIG. 2.
Form of growth curve of tomato leaves in relation to time of year. Each ordinate gives length of leaf half-way through its growth period as percentage of its final length.

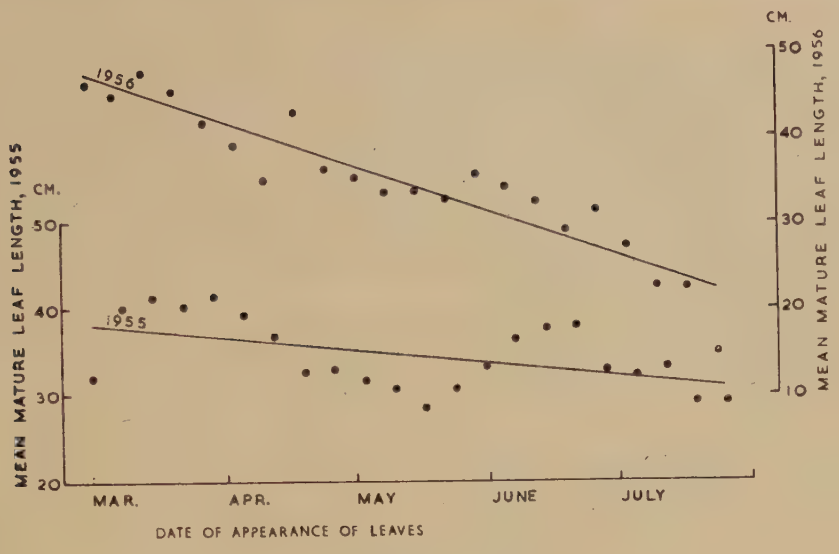

FIG. 3.

Length of mature tomato leaves in relation to time of year.

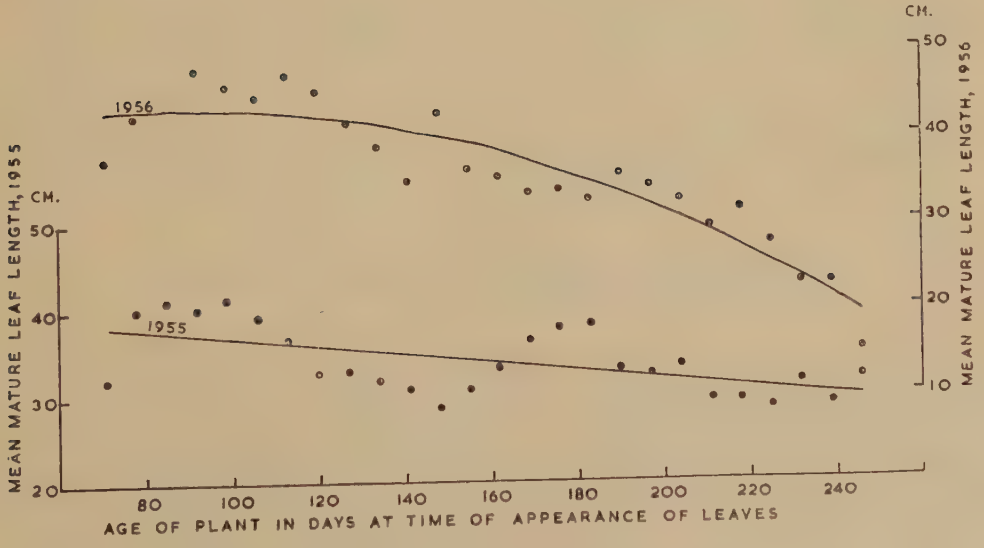

FIG. 4.

Length of mature tomato leaves in relation to age of plant.

(over the range of 120 to 288 days from sowing) and the rate of senescence of leaves. In 1955 the line of closest fit to the data was a first order polynomial with the weekly rate of senescence rising from 0·03 at 120 days from sowing to 2·3 at 288 days from sowing. In 1956, however, this trend did not occur, the line of closest fit being horizontal and giving a weekly rate of senescence of 0·7 over the age range examined.

Consideration of the duration of the growth periods of the 10th to the 82nd leaf on the plants in 1955, and those of the 8th to the 75th leaf in 1956, provided no evidence of any consistent relationship between the position of a leaf on a plant as such (i.e. its number up the main stem, *not* its position relative to an inflorescence) and the duration of its growth period.

Similarly there was no evidence of any relationship between the form of the growth curves of the leaves (expressed as half-period values) and their position on the plant.

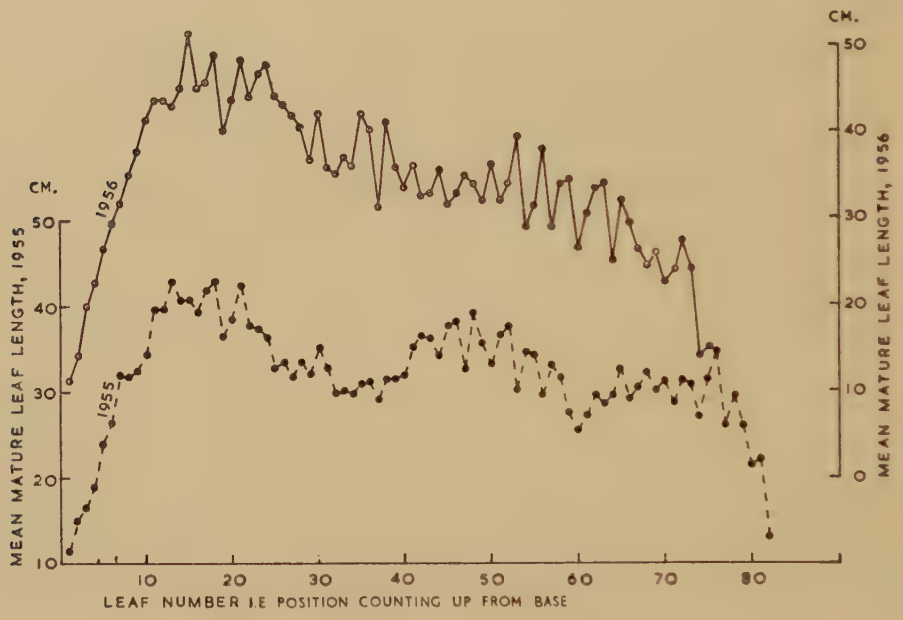

Fig. 5.

Length of mature tomato leaves in relation to position on the stem.

The data in Fig. 5, however, suggest the existence of a relationship between leaf position and final length of the leaf. The mean mature lengths of leaves are shown plotted against the number of each leaf counting from the base of the plant upwards. In both years mature leaf length increased steadily the higher up the plant the leaf was situated until a maximum was reached between approximately leaves 13 and 15. It then declined fairly steadily until about leaves 72–76 when a more rapid decline began. With only one month's difference in sowing dates between 1955 and 1956, it is not possible to determine whether the apparent relationship is really with leaf position or plant age.

Relationship between leaf growth and inflorescence position.

It has been shown for tomato plants allowed to retain first-order axillary shoots that there is a relationship between axillary shoot growth and the position of the axillary shoots relative to the inflorescences on the main stem (Cooper, 1958). To determine whether there is a similar relationship between leaf development and leaf position relative to inflorescence position, the development of the leaf arising immediately below an inflorescence (referred to for convenience as the " inflorescence leaf "), was compared with that of the leaves above and below it. In Table I the mean mature length, the duration of the growth period and the half-period value of 248 leaves have been compared.

TABLE I.

Mean leaf length (cm.), duration of growth period (days) and half-period value (%) of tomato leaves, as affected by position in relation to inflorescence.

	Leaf above inflorescence leaf	Inflorescence leaf	Leaf below inflorescence leaf	Significant difference P=0·05
Mean leaf length	32	38	37	7
Duration of growth period ..	34	36	36	n.s.
Half-period value	69	67	70	n.s.

n.s. = not significant.

None of the comparisons reached significance, though there was a tendency for the leaf immediately above an inflorescence to be smaller than the other leaves, and this tendency approached significance. It is of interest that this tendency in leaf growth is similar to the pattern of shoot growth referred to above, where the shoot arising in the axil of the leaf immediately above an inflorescence is much less vigorous than are axillary shoots arising below the inflorescence.

Relationship between leaf length, duration of growth period, and form of the growth curve.

In Table II are shown the partial correlation coefficients for mature leaf size, duration of the growth period and form of the growth curve.

TABLE II.

Correlations between leaf size, duration of growth period and form of growth curve.

Partial correlation	1955	1956
Leaf size and duration of growth period	+0·24	+0·41
Leaf size and form of growth curve	+0·06	+0·01
Form of growth curve and duration of growth period	+0·47	+0·55

The coefficients for the partial correlation between mature leaf size and the form of the growth curve were non-significant ($P = 0{\cdot}05$). All others were positive and highly significant ($P = 0{\cdot}01$) in both years.

It is thus possible to conclude that leaves that have a long period of growth grow more rapidly initially and attain a larger size than do leaves that have a shorter period of growth. The larger size of such leaves, however, is related, not to their more rapid initial growth, but to the greater length of their growing period.

SUMMARY.

1. A method of estimating leaf area from leaf length is described.

2. No relationship was found between the rate of appearance or senescence of leaves and either the time of the year or the age of the plant.

3. A relationship was shown to exist between the time of the year at which leaves appeared and both the duration of their growth period and the form of their growth curve. The duration of the growth period decreased from March until late May or early June and then increased. Leaves appearing during May and early June made a smaller proportion of their total growth in the first half of their growth period than did leaves appearing earlier or later.

4. There was a tendency for the leaf arising immediately above an inflorescence to be smaller than the leaf arising below an inflorescence.

5. The majority of leaves with a long growing period attained a larger size and made more of their total growth in the first half of their growth period than did leaves with a shorter growing period.

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ROOT DEVELOPMENT OF APPLE TREES IN GRASS AND CLEAN CULTIVATION

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During recent years the use of permanent grass swards for apple orchards has increased greatly. Early workers observed deleterious effects when growing apple trees in grass and concluded that toxic exudates from the grass were responsible for the check to tree growth (e.g. Bedford and Pickering, 1914). Later reviewers re-interpreted the effect of grass as due to competition for nutrients and water. In India, Howard (1925) found that, with plums and peaches, but not with guavas, root growth in the surface soil was restricted by a grass cover, but there was no effect on the growth of deep roots, while Yocum (1937), in the U.S.A., found that root development was restricted under grass sod. Both these authors found that grassing-down depressed the growth of most trees. Experiments at East Malling have shown, however, that with suitable management apple trees can be grown satisfactorily in grass, although the trees may experience a check during the first few years (Rogers *et al.*, 1948). This paper records two studies of the root development of apple trees in permanent grass, compared with that of others in clean cultivation.

STUDY I.

This study comprised eight 16-year-old trees of Cox's Orange Pippin on M.IX growing at East Malling at a spacing of 12 ft. (3½ m.) on the square. Two trees in grass and two of comparable size in clean cultivation were fully excavated ; the roots of two others in grass and of two in cultivation were studied by sampling.

The soil was a well-drained loam 4 to 6 ft. deep, overlying ragstone rock classified as Barming series (Furneaux, 1954). It consisted of 3½ to 4 ft. of light river drift, which from the surface to 18 in. was fine sandy loam and from 18 in. deep to 3½ to 4 ft. deep varied from coarse sand to brickearth. Below this, reddish-brown sandy clay extended to the rock and, for a few inches above the rock, was of chocolate-brown colour.

The average annual rainfall at East Malling is 26·7 in. of which 10·5 in. fall during the growing season (April–September inclusive).

The grass sward was established in April 1944 when the trees were seven years old by sowing with *Poa pratensis* and *Poa trivialis* at 10 lb. per acre. For the first year about 80 per cent. of the sward consisted of annual weeds, but by 1946 a good cover of meadow grass had developed and this lasted till 1949. From 1949 onwards the sown sward became colonized with bent grass (*Agrostis stolonifera*) which increased until, at the time of excavation, in March 1953, the sward consisted of approximately 90 per cent. Agrostis, with a few patches of smooth-stalked meadow grass.

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The " grassed " trees had thus been growing in sward for nine years. The grass was mown six to nine times each year, with the cuttings allowed to lie. The soil between cultivated trees was disc-harrowed at 4–6 week intervals between early March and mid-July, and a weed cover allowed to develop during the autumn and winter months.

Methods.

The two trees in grass and the two in cultivation were excavated together and root plans made of each composite excavation (Figs. 4 and 5). The positions of the nearest roots of neighbouring trees were also recorded. In each pair the first root system was excavated by the " Combined " method of Rogers and Vyvyan (1934). The roots were cut out within blocks and to different depths, weighed ungraded, and retained for reconstruction and photographing. The second root system of each pair was excavated by the " Block " method (Rogers and Vyvyan, 1928), and the suberized roots washed and graded into materials of 0–1 mm. diameter (fibre), 1–8 mm., and thicker than 8 mm. Within metre squares the roots were separated into lots from 0–15 cm. deep, 15–30 cm., 30–50 cm., 50–100 cm. and below 100 cm.

The root systems of two other trees in cultivation and two comparable trees in grass were sampled. Six series of samples, equally spaced, were taken from each tree at 100 cm. from the trunk, i.e. within the main root area (cf. Figs. 4 and 5) ; and at 180 cm. from the trunk, i.e. midway between one tree and another. Samples were taken separately from 0–15 cm., 15–30 cm., and 30–50 cm. in depth, corresponding with the divisions in depth of the whole root excavations. The sample blocks were 20 × 25 cm. in area and were lifted from the face of small trenches by means of a " needleboard " (Coker, 1958) based on the method of Goedewaagen (1948). The sample blocks were soaked in water and the roots washed out, graded into those above and those below 1 mm. diameter, and weighed.

Results.

General characteristics of root growth.

The general habit of the main root systems of these trees was very similar under grass and under cultivation, though this may have been because the main roots had been formed during the first seven years of the life of the plantation, when all the trees were in cultivation. There was no consistent difference in the depth of penetration of roots or in the exploitation of the deeper soil layers (Table I).

Table I.

Percentage of total root weight at different depths.

Depth	Grassed		Cultivated	
	Tree 1	Tree 2	Tree 1	Tree 2
0–30 cm.	75·1	59·2	67·4	66·7
30–100 cm.	20·9	34·7	23·9	26·8
100 cm. and over	4·0	6·1	8·7	6·5

Roots of trees in grass showed scanty growth in some pockets of coarse sand between 70 and 110 cm. deep, but penetrated deeply through pockets of soil of finer texture and spread out in the sandy clay below. This effect was not seen in cultivation.

Under grass, many roots grew upwards from the main root system into the turf, branched freely and often extended horizontally for considerable distances (Figs. 1 and 2). Under cultivation, upward growing roots were continually pruned by disc cultivators at about 12 cm. deep, and they branched profusely immediately below this depth.

Close to the trunk the grass was not mown frequently, and generally grew longer than it did farther away from the tree. Under grass few apple roots grew near the soil surface close to the trunk. In cultivation there were very many shallow fibrous roots (" collar fibre ") in the soil area immediately surrounding the tree trunk which was hand hoed and not disced, and where there was no competition from a grass cover.

In the cultivated plots there appeared to be a layer of compact soil immediately below cultivation depth, but roots penetrated freely into it. It was noted that some main roots had formed just below the usual cultivation depth, had grown to 3–4 cm. thick and extended approximately 2 metres horizontally. On some recent occasion, cultivating implements had penetrated more deeply than usual and cut several main roots which had not only spread widely but also penetrated deeply ; large sectors of the root system had thus been severed (Fig. 3).

Distribution of roots by weight.

Roots of two trees excavated by the " Block " method were graded as described above and gave the results shown in Table II.

TABLE II.

Weight (gm.) of roots of different diameter grades, as excavated by the " Block " method.

Depth	Roots less than 1 mm. diameter (" fibre ")		Roots 1–8 mm. diameter		Roots above 8 mm. diameter		Total roots	
	Grass	Cultivation	Grass	Cultivation	Grass	Cultivation	Grass	Cultivation
0–15 cm. ..	188	87	279	221	0	101	467	409
15–30 cm. ..	192	165	710	858	1,302	1,826	2,204	2,849
30–50 cm. ..	138	92	474	250	220	516	832	858
50–100 cm. ..	131	90	537	228	58	91	726	409
100 cm. and over ..	58	49	217	248	0	0	275	297
Total	707	483	2,217	1,805	1,580	2,534	4,504	4,822

With these trees there was a greater weight of roots 0–1 mm. diameter at all depths on the grassed than on the cultivated tree, and less weight of roots of the thickest category.

The weights of roots less than 1 mm. diameter, at different depths and at different distances fron the trunk, were expressed as percentages of the total on each tree (Table III).

Table III.

Percentage distribution of fibrous roots (0–1 mm.).

Depth	Within 1-metre square		Area between 1- and 3-metre squares		Outside 3-metre square		Total roots	
	Grass	Cultivation	Grass	Cultivation	Grass	Cultivation	Grass	Cultivation
0–15 cm. ..	1·9	8·9	14·4	7·2	10·3	1·8	26·6	17·9
15–30 cm. ..	2·7	5·9	17·4	18·4	7·1	10·0	27·2	34·3
30–50 cm. ..	2·7	3·8	11·5	11·2	5·3	4·1	19·5	19·1
50–100 cm. ..	2·0	1·8	10·7	13·3	5·8	3·4	18·5	18·5
100 cm. and over ..	1·1	0·0	2·8	9·6	4·3	0·6	8·2	10·2
Total ..	10·4	20·4	56·8	59·7	32·8	19·9	100	100

The above table shows that the tree in grass had a smaller proportion of fibrous roots close to the trunk than the tree in cultivation, and a larger proportion of its fibrous roots outside the 3-metre square. These differences were most strongly marked in the 0–15 cm. depth layer.

Root spread and tree-to-tree competition.

The root plans show the extent of root spread and the relations between neighbouring root systems (Figs. 4 and 5). The ground area occupied by the roots was estimated by counting the half-metre squares which contained roots (Table IV).

Table IV.

Area (sq. metres) of root spread of excavated trees.

	Grass	Cultivation
Tree 1	13·75	10·50
Tree 2	14·25	10·00

Under grass practically the whole soil area contained roots, and roots from adjacent trees commonly met and turned laterally or downwards at the periphery. Under clean cultivation a few roots extended as widely as under grass, but they appeared to be less branched and the root systems did not completely cover the soil area.

PLATE I

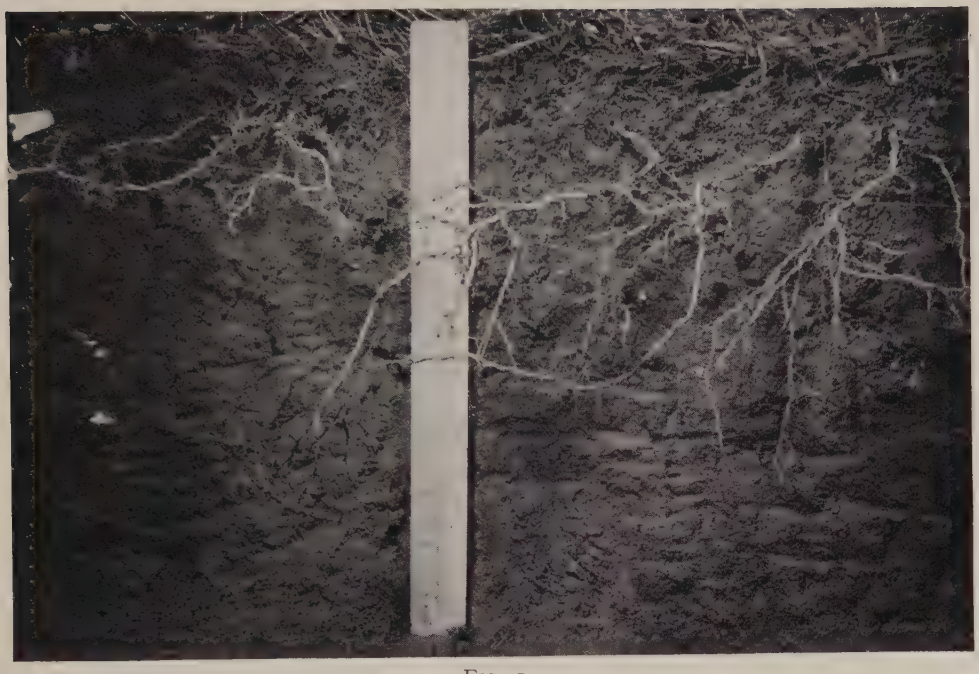

Fig. 1.
Fibrous roots of apple growing in the turf close to the soil surface.

Fig. 2.
Root system of Cox's Orange Pippin on M.IX under grass, reconstructed after excavation. Note that many fine roots have grown toward the soil surface.

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PLATE II

FIG. 3.

Root system of a sister tree to that shown in Fig. 2, but in clean cultivation, reconstructed after excavation. Note that a large section of the root system has been cut (see arrow) by a cultivator penetrating more deeply than usual.

FIG. 4.

Roots of 16-year-old Cox apple trees on M.IX in grass.
The grid consists of 1-metre squares; the broken line represents branch spread; the dotted lines represent roots of adjacent trees; the numbers indicate the depth in cm. of marked roots.

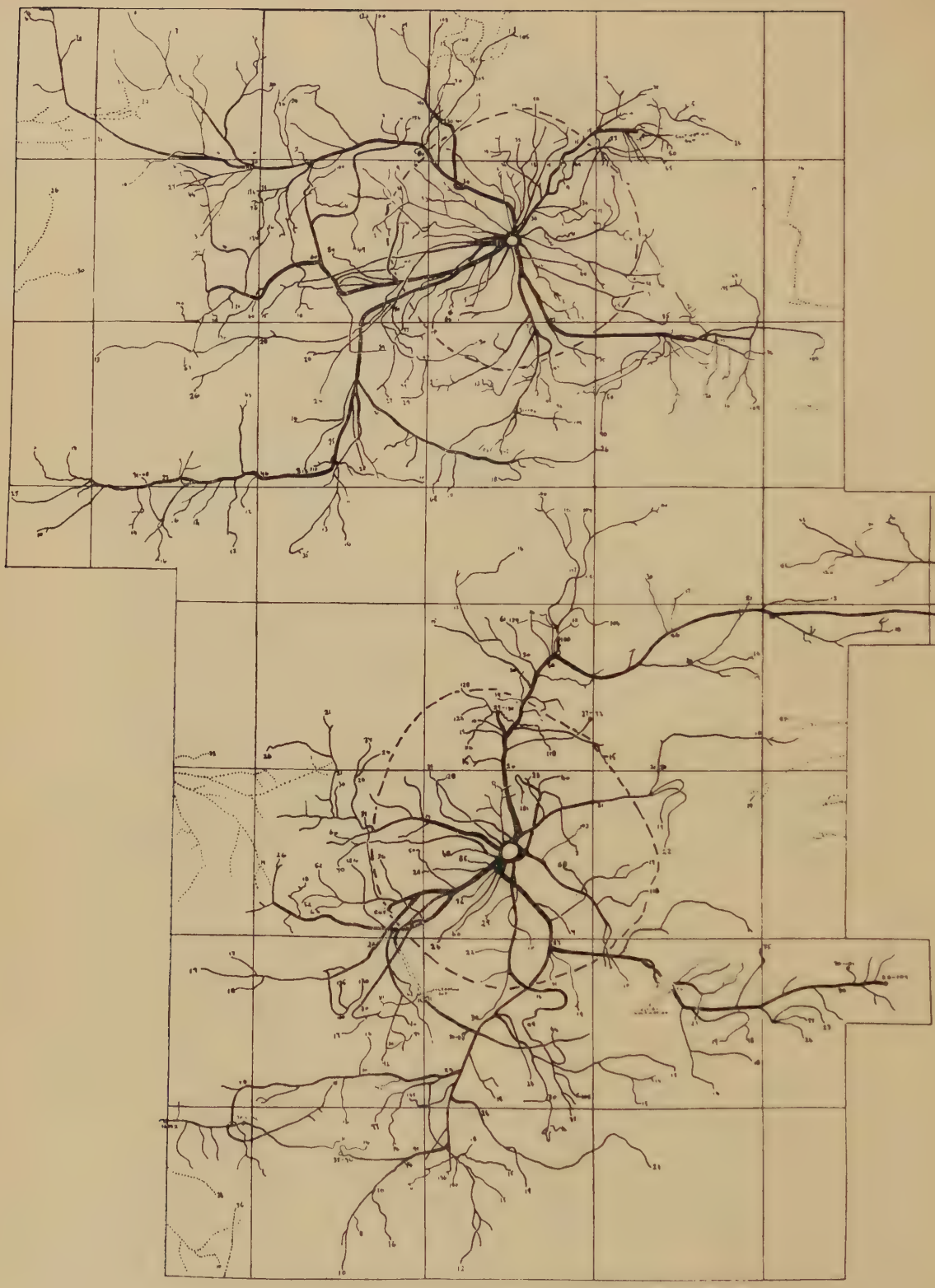

FIG. 5.
Roots of 16-year-old Cox apple trees on M.IX in cultivation.
See notes to Fig. 4.

The stem/root ratio.

Rogers and Vyvyan (1934) found that the stem/root ratio was less on a poor sand than on a sandy loam soil and considered it an index of soil fertility. Heinicke (1921) studied the effect on stem/root ratio of grass and cultivation treatments and the use of nitrogenous fertilizers. He found that a grass cover reduced the ratio of stem to root, except where additional nitrogenous fertilizer was applied. Relevant data for the trees excavated are given in Table V.

TABLE V.

Fresh weight (gm.) of stem and roots of excavated trees.

	Grass		Cultivation	
	Tree 1	Tree 2	Tree 1	Tree 2
Stem weight	7,140	10,580	9,607	11,399
Root weight	2,925	4,504	3,493	4,822
Stem/root ratio	2·44	2·33	2·75	2·36

It would appear that grassing down had no appreciable effect on the stem/root ratio of these four trees.

Root sampling data.

The complete excavations described above strongly suggested that the root development of apple trees had been modified by a long-term grass sward so that, as compared with clean cultivation, the area of root spread was greater, there were more fibrous roots, especially on the periphery of the root system, and many fibrous roots developed near the soil surface. The data in Table VI were provided by sampling two other trees under each treatment and are means of twelve samples (six per tree) at each position and depth.

TABLE VI.

Fresh weight (gm.) of roots less than 1 mm. in diameter.

Depth	100 cm. from tree		180 cm. from tree		Means of samples at two positions	
	Grass	Cultivation	Grass	Cultivation	Grass	Cultivation
0–15 cm.	0·63	0·43	0·83	0·43	0·73	0·43
15–30 cm.	0·98	0·87	0·92	0·29	0·95	0·58
30–50 cm.	0·94	0·52	0·78	0·09	0·86	0·31
Total	2·55	1·82	2·53	0·81	2·54	1·32

This series shows trends similar to those already noted on whole-root excavations.

STUDY II.

During January–April 1956, root sampling studies were carried out on 46-year-old Worcester Pearmain apple trees which had grown in permanent grass since 1940, and on comparable trees which had been under grass during the period 1940–43 and under clean cultivation since that time. The trees were spaced at 25 ft. ($7\frac{1}{2}$ m.) along the line of treatments. The soil was a sandy loam comparable in texture to that of Study I. It was, however, much more shallow beneath the sampled trees, being little over 50 cm. deep over free draining ragstone rock. Eight typical trees were sampled from each treatment and on each tree samples were taken at 1·5 and 3·5 metres from the trunk. The former distance was taken as being well within the root zone and the latter as midway between trees, where differences in root competition might show up. Sampling was repeated to North and South of each tree and the samples were taken in the way described earlier in this paper. The data are presented in Table VII.

TABLE VII.

Mean fresh weight (gm.) of apple roots less than 1 mm. in diameter.

Depth	Samples 1·5 m. from tree		Samples 3·5 m. from tree		Means of samples at the two positions	
	Grass	Cultivation	Grass	Cultivation	Grass	Cultivation
0–15 cm.	4·35	0·84	4·60	0·72	4·48	0·78
15–30 cm.	1·83	0·71	2·60	1·20	2·15	0·96
30–50 cm.	1·68	0·63	1·54	0·64	1·61	0·63
Totals	7·86	2·18	8·74	2·56	8·24	2·37
Ratio of total root weights					3·47	1·0

An analysis of variance was carried out on the mean data for the two distances from the trunk. The weight of roots less than 1 mm. diameter was significantly greater at all depths under grass than under cultivation ($P<0·001$).

DISCUSSION AND CONCLUSIONS.

The root growth of a fruit tree may be modified by a grass sward : (a) by the absence of cultivation allowing tree roots to grow into the surface soil ; (b) by direct competition of the sward for nutrients and water ; or (c) by the indirect effects of sward on nutrient availability or soil structure.

In the experiments described, grass apparently had no effect on the pattern of the main scaffold root system or on the depth of exploitation of the profile. There were, however, considerable differences in other respects.

Under cultivation, roots growing upwards had been pruned in successive years to approximately 12 cm. (5 in.) deep by cultivating implements and had formed a layer of fine roots just below this depth. Under grass, the upward growing roots extended near to the soil surface where they either branched or continued growth in a horizontal direction.

Roots of the excavated trees in cultivation did not occupy the entire soil area, and root plans showed that the root systems of the trees excavated from grass covered a larger superficial area than those of trees from cultivation. This was not, apparently, due to shorter extension of main roots under cultivation, for some had extended as far as, or farther than, roots in grass. The roots in grass appeared to occupy the soil more fully as a result of more extensive branching. This suggestion of increased branching was supported by data on grading of roots excavated by the " Block " method, which showed an increase in the weight of fine roots and a decrease in the weight of thick roots at all depths under grass.

Under grass there was a greater proportion of fine roots near the periphery of the root system and this can be associated with the greater area of spread of the root system, and with the reduction in root development near the trunk due to competition from long grass around it, which was cut less frequently than the rest of the sward.

The data from the 1953 sampling studies showed similar trends. On the trees sampled, there was under grass an increase at all depths in the weight of roots less than 1 mm. in diameter, particularly with the samples taken farther from the tree. The data from the 1956 sampling studies gave similar results. By contrast with the 1953 sampling studies, samples taken midway between trees and those taken closer to the trunk were similar for each treatment, indicating that on this Plot roots of trees under both treatments explored the entire soil block.

Both root excavations and sampling studies lead to the conclusion that, under an old grass sward, apple roots not only colonize the uncultivated soil right up to the soil surface, but they branch more extensively and create a denser and more fibrous root system at all depths. Rogers (1939) showed that, if the soil dries beyond a certain point, the production of absorbing roots declines. Since the fine roots are the main seat of origin of absorbing roots, it is likely that, during periods in the growing season when the soil is as moist under grass as under cultivation, a tree in grass carries more absorbing roots than one in cultivation owing to the greater amount of fine suberized roots present. Under drying conditions water loss often takes place more rapidly under grass than under cultivation, so that the production of absorbing roots would fall off more rapidly under grass. Thus a time would come when the more fibrous root system in grass would fail to offset the poorer production of absorbing roots due to the drier soil. This fits in with observations that, in general, trees in grass grow well in moist soil but relatively poorly in soils deficient in moisture.

The changes in rooting found are probably related to the recovery of apple trees from the check to growth associated with grassing down and may, entirely or in part, compensate for the competition for moisture and nutrients which exists between grass and tree. The presence of the roots in the surface soil layers may enable the tree to utilize some of the moisture provided by light summer rains, much of which, under cultivation, would be held unavailable in the disturbed surface layer of soil and lost to the air by evaporation. Where roots of cultivated trees are not already competing with each other, the greater area of soil explored by roots of similar trees under grass would provide access to rain over a wider area than to trees under cultivation. In addition, the more dense fibrous root system under grass may well provide a greater absorbing surface and may thus more efficiently exploit soil reserves of moisture and nutrients. In general, soil analyses show a higher level of availability of nutrients near the soil surface than deeper down the profile ; the shallow

tree roots found under grass would utilize such nutrient distribution to the best advantage.

If the old orchard sward beneath the excavated and sampled trees had been ploughed to only 6 in. (15 cm.) deep, it would have destroyed 25–53 per cent. of the tree's fibrous roots, which were growing in soil generally high in available nutrients. The author suggests that the ploughing up of old orchard swards during the life of the trees should be avoided as far as possible, or the possibility of a temporary check to tree growth accepted if they are growing well. Shallow cultivation with a rotary cultivator might be less damaging. However, where trees have been grassed down on soils with insufficient moisture reserves, and the grass ploughed up after the trees are thereby checked, the destruction of tree roots would probably be more than offset by the beneficial effect of releasing the tree from competition with the grass. The importance, where cultivating, of doing so to a *consistent* depth is emphasized by the damage done to horizontally spreading scaffold roots by one cultivation which penetrated more deeply than usual and severed large sectors of deep and shallow roots from the tree.

SUMMARY.

1. The rooting of four 16-year-old apple trees grown in grass for nearly ten years is compared with that of similar trees grown in clean cultivation throughout ; both excavation and sampling methods were used. Roots of sixteen other trees were studied by sampling.

2. Many roots grew up into the surface soil under grass and into the turf itself, and ramified there. Under cultivation, few roots grew near the surface.

3. Trees in grass had a more branched root habit and more fibrous roots at all depths, than those in cultivation.

4. The general conformation of main roots and the depth of root penetration were similar under grass and cultivation.

5. Under cultivation some trees studied did not fully explore the soil block, but comparable trees in grass explored a greater area of soil. Other larger cultivated trees were found to be exploiting the entire soil area.

6. The relation of these differences in root development to tree response and to orchard practice is discussed.

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THE EFFECT OF SPLIT LEAF BLOTCH AND NETTLEHEAD VIRUS DISEASES ON THE YIELD OF FUGGLE HOPS

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Fuggle constitutes 73 per cent.* of the total hop acreage in England and it is only in this variety that the virus diseases, split leaf blotch and nettlehead, are widespread. Of the two, nettlehead is less common, but it has a more severe effect on hop plants and has generally been considered the more serious disease ; but split leaf blotch is so prevalent in Fuggle hops that, even if its effect on yield were slight, the total loss to the industry would be considerable. In practice, however, few growers take any control measures against split leaf blotch, although they attempt to eradicate nettlehead by removing affected plants.

The effects of these diseases on yield have not previously been measured, although Wilkinson (1947) noted an obvious reduction of crop from plants severely affected by split leaf blotch, and Keyworth and Davies (1946) stated that plants with severe nettlehead bear only a few distorted cones. The trials reported below were undertaken to measure the effects of these two diseases on the weight of kiln-dried hops and on soft resin content, the latter being probably the most important hop constituent in brewing.

Experimental procedure.

Two trials were carried out, A in 1955 and B in 1956, in parts of established Fuggle plantations planted on a 6-ft. lattice and trained on the umbrella system (Burgess, 1956). Large trial areas of 1·6 and 7·0 acres in 1955 and 1056 respectively were used to compensate for soil variation, the soils of both plantations being rather heavy and subject to waterlogging.

In each trial a comparison was made between yields from symptomless plants and those showing symptoms of either split leaf blotch or nettlehead. Plants affected with nettlehead were selected regardless of the severity of the disease, but with split leaf blotch only the two more severe forms, known to be graft transmissible (Keyworth, 1951), were included.

Trial A, 1955.

An arbitrary selection was made, five days before picking, of 25 symptomless plants, 25 plants showing split leaf blotch symptoms and 25 plants showing nettlehead symptoms. The selected plants were distributed evenly over the trial area. For various reasons some of them were not sampled and those with no crop were

* Figure for 1956 from " Hop Report, 1956 Season ", by Messrs. Wigan Richardson & Co.

ignored ; the actual number considered in each category is shown in Tables I and II. The hops were picked on the same day, plants in each category being taken in rotation to minimize the variation due to changes in moisture content through the day. The green-hop yield per plant was measured and a weighed sample of green hops from each plant was dried (in a muslin bag) in a conventional hop kiln. The weight of these dried hops will be referred to as dry-hop weight, i.e. containing approximately a 10 per cent. moisture content, which is the usual requirement for satisfactory storage of hops (Burgess, *loc. cit.*). The yield of dry hops from each plant was calculated from the measured total green weight, sample green weight and sample dry-hop weight. The soft resin content of each dried sample was determined by the method of Briant and Meacham (1897).

Trial B, 1956.

The procedure followed in this subnormal cropping year was essentially similar to that in Trial A, except in the selection of sample plants. Random samples, one of 25 plants showing split leaf blotch and another of 25 plants showing symptoms of nettlehead, were taken from a symptom record made in June, before the potential crop could be assessed. Each diseased plant was then paired with a symptomless control, taken as the next but one plant to the north ; if this was missing, then the next symptomless plant the same distance away in a clockwise direction around the diseased plant was used.

Results.

The dry-hop weights and soft resin values were adjusted (by analysis of covariance) to a 10 per cent. moisture level (Tables I and II) and these figures used for analysis. In each trial the mean dry-hop yields from plants showing symptoms of either split leaf blotch or nettlehead were much lower than from symptomless plants ($P < 0{\cdot}001$). In addition the mean soft resin content was significantly reduced in cones from plants with symptoms of nettlehead (Trial A, $P < 0{\cdot}001$; Trial B, $P < 0{\cdot}05$) ; from plants with split leaf blotch symptoms there was inconclusive evidence that such a reduction occurred, the differences being just significant in Trial A but not significant in Trial B.

Table I.

Trial A. Mean dry weight and soft resin yield of hops, adjusted to 10 per cent. moisture, as affected by virus diseases.

	Plants with nettlehead	Plants with split leaf blotch	Symptomless controls
No. of samples	21	25	24
Dry weight (gm. per plant)	25·8**	360·7**	589·1
Soft resin (%)	7·1**	7·8*	8·4

** Differences between diseased and control significant at $P<0{\cdot}001$.
* Difference between diseased and control significant at $P<0{\cdot}05$.

Table II.

Trial B. Mean dry weight and soft resin yield of hops, adjusted to 10 per cent. moisture, as affected by virus diseases.

	Plants with nettlehead	Symptomless controls	Plants with split leaf blotch	Symptomless controls
No. of samples	20	20	23	23
Dry weight (gm. per plant) ..	92·2**	398·0	222·1**	424·2
Dry weight (cwt. per acre) ..	2·2	9·5	5·3	10·1
Soft resin (%)	8·2*	9·0	8·1	8·4

** Differences between diseased and control significant at $P<0.001$.
* Difference between diseased and control significant at $P<0.05$.

DISCUSSION.

It is suggested that, as these plants were apparently uniform except for disease symptoms, the measured reductions in yield can conclusively be ascribed to the diseases. Although the severe effect of nettlehead on crop weight and resin content was predictable, the considerable reduction caused by split leaf blotch was not expected. Thus, in Trial B, there was a 50 per cent. reduction in crop weight from plants showing symptoms of the latter disease, the yield representing only 5·3 cwt. per acre compared with 10·1 cwt. per acre from symptomless plants. In fact the effect of the virus may be greater than this, as the intermittent appearance of symptoms (Keyworth, 1951) probably allowed some infected plants to be included among the controls.

The effect of split leaf blotch on yield provides a striking instance of a virus disease causing a large and sometimes unexpected crop loss. In measures devised to reduce the incidence of hop diseases, due attention has been paid to the more conspicuous nettlehead, and Fuggle sets certified for freedom from this virus are obtainable from isolated nurseries under the Ministry of Agriculture's certification schemes. But the position is less satisfactory for split leaf blotch, mainly because no reliable indicator plants are known, and at present no Fuggle sets unequivocally free from this virus are available to the hop grower.

The performance of virus-free stocks in commercial plantations would depend upon the subsequent rate of virus spread, about which little is known ; it may be rapid, as Keyworth (*loc. cit.*) refers to " the apparently remarkable increase in incidence of split leaf blotch since it was first recorded in 1933 ", an increase which he did not attribute to better recognition.

SUMMARY.

In two trials comparing yields from plants showing symptoms of either split leaf blotch or nettlehead with those from symptomless plants, there was a reduction of about 50 per cent. in the weight of hops from plants with split leaf blotch and of over 75 per cent. from plants with nettlehead. In view of the prevalence of split leaf blotch in the widely planted variety Fuggle, it is suggested that this must be regarded as one of the most serious diseases of hops.

ACKNOWLEDGMENTS.

The writer wishes to thank Arthur Guinness Hop Farms Ltd. for accommodating these trials on their Bodiam Hop Farm, and the members of their staff who have assisted in this work, including those responsible for the experimental picking and for the moisture and soft resin analyses. He is particularly indebted to the Managing Director, Mr. J. F. Brown, for his personal help and encouragement throughout.

Miss S. V. Cunliffe of Arthur Guinness Son & Co. (Park Royal) Ltd., and Dr. G. H. Freeman of East Malling Research Station were responsible for the statistical design and analysis of these trials.

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TRANSMISSION OF A VIRUS CAUSING STAR CRACK OF APPLES

By A. F. POSNETTE and R. CROPLEY
East Malling Research Station, Kent

JENKINS and Storey (1955) reported an unhealthy condition of apple trees as being widespread, but not prevalent, in East Anglia. Affected trees began growing late in the spring ; bark lesions developed on one-year-old wood and die-back of leader shoots was common in winter, followed by vigorous growth from buds lower down the shoots (Fig. 1). The number of flowers and of fruits was reduced and many of the mature apples were marked by star-shaped cracks. These authors found wood and fruit symptoms in fifteen orchards and fruit symptoms in fourteen others. The condition was most common on Cox's Orange Pippin, but several other varieties were seen with fruit symptoms. No fungal pathogen was isolated from diseased wood, and it was suggested that a virus was responsible.

Transmission tests.

In the spring of 1954 scions from two affected Cox trees in Essex orchards, one at Langham (isolate 36) and the other at Colchester (isolate 37), and from a healthy tree at East Malling were grafted in sets of five each on to M.VII rootstocks as follows :

1. Cox from a normal East Malling tree,
2. Cox from an affected tree,
3. Double grafts : Cox from a healthy tree (as in 1) with an " intermediate " scion from an affected tree between the M.VII rootstock and the healthy Cox scion.

In the spring of 1955 trees of sets 2 and 3 developed tip die-back and cankers around the buds. Leafing out was delayed and in the autumn young leaves on terminal shoots were reduced in size, cupped and chlorotic (Fig. 2) ; these symptoms have recurred each year. The die-back and bud lesions usually began on the one-year-old shoots during January and the bud lesions developed rapidly during the next three months (Fig. 3). Bark symptoms induced by the Langham isolate have been more severe than those induced by the Colchester isolate ; the former has delayed blossoming by 14–21 days and the latter by 7–10 days (Fig. 4). In 1958 fruits matured on the five-year-old trees and those on the control (set 1) trees were normal. Only one tree of the Langham isolate fruited : five apples matured, two of which had star cracks. All trees of the Colchester isolate fruited, and many of the apples developed star cracks (Fig. 5).

A similar experiment was made in 1954 using scions from an affected Bramley's Seedling tree. Slight die-back and canker symptoms were produced on the previously healthy Bramley scions and some of the fruits had star cracks (Fig. 6).

PLATE I

Fig. 1.

A Cox's Orange Pippin tree with star crack disease. Note delay in flowering and many shoots arising from the main branches.

[face p 126

FIG. 2.

Left: healthy terminal growth of Cox's Orange Pippin. *Right:* comparable shoot showing yellow cupped leaves caused by star crack infection.

FIG. 3.

Canker developing beneath bud on one-year-old shoot of Cox's Orange Pippin.

FIG. 4.

Delay in leafing and flowering of Cox's Orange Pippin.
Left: healthy tree; *centre:* infected with star crack isolate 37; *right:* infected with star crack isolate 36.

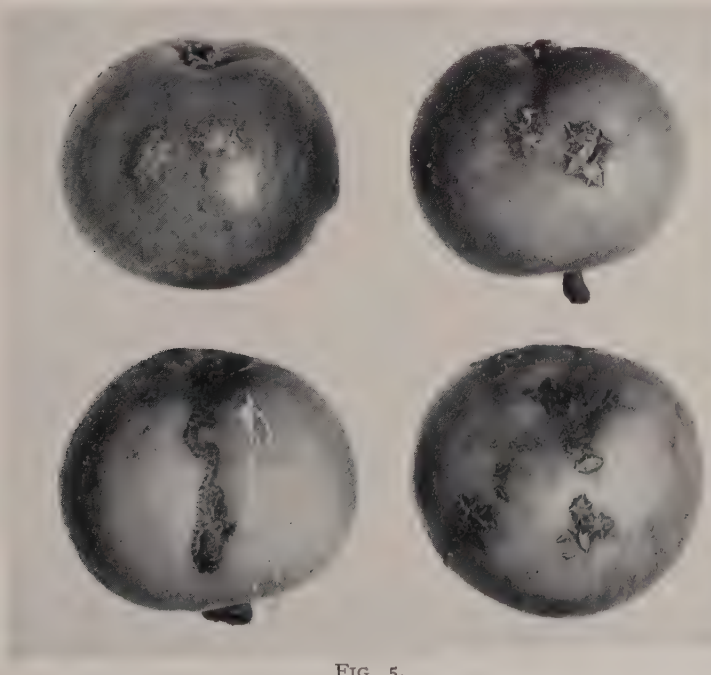

FIG. 5.

Cox's Orange Pippin fruits from tree inoculated with star crack virus (isolate 37).

FIG. 6.

Bramley's Seedling fruits from tree inoculated with star crack virus.

Comparison of eighteen isolates.

The marked differences in the severity of the two isolates from Cox trees in Essex suggested that a wide variation in virulence might exist. In the summer of 1955 budwood from eighteen trees with suspected star crack symptoms was used for propagating sets, each of 5 trees, as follows :

1. Bud from affected tree on M.II rootstock,
2. Bud from a healthy (East Malling) Cox tree on M.II rootstock, with an " infector " bud from an affected tree inserted in each stock 2 in. below the healthy bud. The shoots which grew from these infector buds were cut off in the following spring and the trees planted out after one year's growth for further observation, with two healthy Cox trees planted between each set of five inoculated trees.

The symptoms that have developed on the double-budded plants in the experiments up to the end of 1958 are summarized in Table I. The wood- and leaf-symptoms on these double-budded Cox trees have been slightly less intense than those on the plants raised from buds of the affected Cox trees. This suggests that the virus has moved or multiplied slowly in the indicator scions.

The results in Table I show that wherever die-back and bud canker symptoms have developed, star cracks have formed on the fruits. Two isolates (67 and 79) have induced fruit symptoms with only very mild bark symptoms, while one isolate (77) has induced fruit symptoms only.

All of the trees raised from scions from orchard trees with only die-back and no fruit symptoms are normal, and no abnormalities have occurred on the plants inoculated with buds from these sources. There is so far no evidence of transmission to Cox from the two James Grieve trees with abnormal fruits (isolates 80 and 80A).

DISCUSSION.

These preliminary results confirm the orchard observations of Jenkins and Storey (*loc. cit.*) that Cox trees that are late in leafing out and show die-back and bud cankers always have star-cracked fruits ; some trees, however, without delay and wood symptoms bear star-cracked fruits. No virus causing die-back has been transmitted from trees with die-back and *normal* fruits, so that other factors are probably responsible for the unhealthy condition of these trees. The differences between the " isolates " in the severity of symptoms suggest that there are several strains of the virus, all of which cause fruit cracking but only the more virulent ones affect also bark and leaves.

The possible relationship of star crack with other virus diseases of apple is not known. Cox trees infected with mild, intermediate and severe strains of apple mosaic virus and with a vein-clearing virus (Posnette and Cropley, 1956) have shown no bark lesions or fruit cracking. Chat fruit and rubbery wood are not associated with the disease, as Lord Lambourne plants inoculated by double budding with the most severe isolate (36) of star crack from Cox have not developed symptoms of chat fruit, rubbery wood or star crack. False sting in Canada (Hockey, 1941), green crinkle in New Zealand (Atkinson and Robbins, 1951), and rough skin in Holland (Mulder, 1955) are virus diseases of apples causing fruit symptoms similar to star

Table 1.

Summary of transmission experiments with Cox's Orange Pippin.

Symptoms on orchard sources of inoculation	Isolate number	Symptoms on inoculated trees			
		Delay in leafing out in spring	Die-back and canker	Terminal leaves in autumn	Fruits
Cox : die-back, bud cankers, star crack fruits	36	Severe	Severe	Yellow, cupped	Star crack
	69	,,	,,	,,	,,
	70	,,	,,	,,	,,
	62	Moderate	Moderate	,,	,,
	37	,,	,,	,,	,,
	63	Slight	,,	,,	,,
	50	Not recorded	,,	,,	,,
Cox : die-back, bud cankers (young trees, no fruit) ..	60	,,	,,	,,	,,
American Mother : star crack fruits	67	None	Mild	,,	,,
Cox : slight die-back, star crack fruits	79	,,	Very mild	Slightly cupped	,,
Cox : star crack fruits, no die-back	77	,,	None	Normal	,,
Cox : die-back, normal fruits	73	,,	,,	,,	Normal
Cox : die-back, bud cankers, normal fruits	C2F9	,,	,,	,,	,,
James Grieve : fruits russeted and cracked	80	,,	,,	,,	,,
James Grieve : fruits russeted, spotted and cracked	80A	,,	,,	,,	,,
Beauty of Bath : small cracked fruits	78	,,	,,	,,	,,
Cox : die-back and proliferation of shoots	48	,,	,,	,,	,,
Cox : proliferation of shoots, normal fruits	68	,,	,,	,,	,,

crack, but bark cankers have not been reported and the experimental data available are insufficient for reliable comparisons to be made between these diseases and star crack.

SUMMARY.

A virus causing star-shaped cracks on apple fruits was transmitted by grafting from infected to healthy Cox trees, and from an infected Bramley tree to healthy Bramley trees. Other symptoms, produced by some isolates but not by others, are delay in leafing out in the spring, die-back of one-year-old shoots, lesions around the buds, and cupped, chlorotic leaves at the tips of terminal shoots in the autumn.

ACKNOWLEDGMENTS.

Mr. J. E. E. Jenkins kindly provided Fig. 1. The other photographs were taken by Mr. E. Yoxall Jones.

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BOOK REVIEWS

ROSES. By F. Fairbrother (London: Penguin Books Ltd. 1958. Pp. 180, illus. Price 5s.)

We have often commented on the value of the Ministry of Agriculture's bulletins, packed as they are with up-to-date information, to the commercial horticulturist. Here, for the amateur, is the first of a similar series of books, well within the reach of his pocket. The Penguin Book Company and the Royal Horticultural Society, with whose collaboration the series is to be produced, are to be commended for their enterprise, which we anticipate will be well rewarded.

Those who would like to grow good roses, among whom I would include myself, will be grateful to Mr. Fairbrother, Deputy President of the National Rose Society, for all the information he has given them out of his long experience. I know that my own copy will be frequently consulted. T.N.H.

JUST WEEDS. New expanded edition by E. R. Spencer. (London : Charles Scribner's Sons Ltd. 1957. Pp. 333, illus. Price 32s. 6d.)

The chief purpose of this book on American weeds, most of them known elsewhere, as enunciated by the author, is " to teach and to make interesting to any and all readers a few of the common forms of nature ". It must be admitted that Professor Spencer seems to have great affection for many of the species described, for their many and curious names and for their endearing characteristics. Thus of bedstraw (*Galium aparine* L.) he writes : " The roots make a red dye, and a wash made by boiling the stems is said to be good for sunburn and freckles." At the same time he always includes accurate botanical descriptions, and does not neglect to devote ten pages to weed control by cultural and chemical means. The 102 illustrations by Emma Bergdolt are both decorative and useful for identification purposes.

D.A.

BUSH PEACHES. By C. P. H. Wilson. (London : W. H. & L. Collingridge Ltd. 1958. Pp. 140, illus. Price 42s.)

The author of this delightful book on peaches admits that " most of the varieties grown in England as bush trees suffer from die-back and bud abscission ", and that his own young trees " have been growing into die-back " as they mature rather than growing out of it. It would be wrong, therefore, to regard this book as a guide to the successful culture of peaches, because until die-back, a trouble of as yet unidentified cause, can be controlled, it remains the chief factor limiting commercial peach growing in England. The book, however, does draw together what is known about peaches and their culture, from ancient and modern publications. In this the author has been extraordinarily successful, and he seems to have missed little of modern research on this crop. Attention is drawn to the diversity of form of leaves, glands, flowers,

buds, fruits and nodes, as well as to the practical points of propagation, pruning, soils, manuring, fruit thinning, the control of pests and diseases, choice of variety, and cold injury and requirements. It may be a little surprising that there is no reference to split-stone, a severe trouble of fruit in some seasons and one that the author is likely to meet as his own trees mature. The suggestion that " hot water treatment " of budsticks can deal with virus diseases in general is misleading. These are small blemishes, however, in a book that achieves a high standard of accuracy and presentation and which, once picked up, is difficult to lay down.

H.B.S.M.

SPRAYING TECHNIQUE IN AGRICULTURE. S.C.I. Monograph No. 2. (Society of Chemical Industry, 14 Belgrave Square, London, S.W.1. 1958. Pp. 117, illus. Price 18s.)

The natural desire of growers of crops requiring spraying to reduce the amount of water used, and hence the time taken up in filling tanks as well as in the actual spraying, has led to vigorous attempts to produce machinery capable of distributing small volumes of spray over quite large target areas. This has been largely on an *ad hoc* basis, although several research groups have been at work on the principles required for success. As the chairman of the symposium reported in this book pointed out in his introductory remarks, the terms low-volume and concentrate spraying mean different things to different people ; even at the end of the meetings this was still true. As soon as one gets away from complete cover (spraying to run-off), the size of the crop plant in relation to the unit of area leads to a need to specify the crop when trying to express the rate of application, low-volume on a tall crop (e.g. fruit trees) being high-volume on a low crop such as emerging cereals. The term concentrate may mean anything from twice the " normal " rate of application to one hundred times in the case of lime sulphur used undiluted. The present reviewer doubts whether the term low-volume should be applied, as it was by several speakers in this symposium, to spraying trees at 50–75 gallons per acre when the same control can be obtained at 10–20 gallons per acre of a proportionately stronger wash, using a suitable machine. However, the problems associated with producing truly low-volume machines are tending to shift the interest in research circles to rather larger volumes, and the term low-volume will doubtless attach to these.

The symposium, which extended over four sessions, covered much ground, and was contributed to by biologists, chemists, engineers and growers. Thus the basic needs for disease control, especially on fruit trees, as well as the problems of producing machines capable of putting droplets of the right size all over a tree, at an economic cost, were well brought out.

Pest control with small volumes of concentrated sprays has not been so thoroughly studied as the control of apple diseases by lime sulphur. But, as J. T. Martin pointed out, pests should be controlled more readily than diseases, and the success of truly low-volume spraying against apple sawfly, reported by G. H. L. Dicker, gives great hope that this may be so.

The printers have produced a pleasing format and binding. The book is not free from errors, but it provides in handy form a summary of knowledge and experience up to the end of 1956, and should be widely read.

A.H.M.K.

THE COUNTY OF ANGLESEY, SOILS AND AGRICULTURE. By E. Roberts. Agricultural Research Council ; Memoirs of the Soil Survey of Great Britain. (London : H.M. Stationery Office. 1958. Pp. 116, illus. Price 10s.)

Much credit is due to Evan Roberts for the masterly manner in which the soil survey of Anglesey has been produced and for collecting together the large amount of data to form a clear and readable presentation. This publication is in many ways a fitting reminder of the interest taken in this field of study by the late Professor G. W. Robinson after his appointment to the University College of North Wales at Bangor.

The memoir points out the great advance that has been made in soil-survey methods since those early days. The first soil maps were based on geological formations, soil texture and drainage conditions. The later adoption of " soil series " as a mapping unit emphasizes how soils, formed in similar ways and having the same properties, can be grouped together and that these groups can again be subdivided into " types " according to the old basis of classification.

The soil series are described in great detail and an excellent coloured map is included. The publication should not only be of interest to agricultural students and advisory officers, but will undoubtedly enable the farmer to look on his farm in a more intelligent manner by correlating his many observations and problems with soil types. The results of a few fertilizer experiments on definite soil types are quoted and no doubt the survey will become increasingly useful as more data are accumulated on this point.

The history of agriculture on the island is especially interesting and the tables and figures giving the fluctuations of acreages under different crops and the variation in the number of livestock from time to time are a most valuable contribution. The reader may feel that the pattern of farming as practised at the present time has not received the attention it really deserves.

The reviewer noted very few mistakes. Attention should be drawn to the error in the size of clay particles in the analytical data on soil profiles.

The memoir is very well presented and should stimulate much more general interest in soil as the basic material in all agricultural production.

J.O.J.

PUBLICATIONS RECEIVED.

JAHRBUCH 1955/56. (Deutsche Akademie der Landwirtschaftswissenschaften zu Berlin. 1957. Pp. 555.)

BOOKS ON AGRICULTURE AND HORTICULTURE. Ministry of Agriculture Bulletin No. 78. Fourth edition. (London : H.M. Stationery Office. 1958. Pp. 96. Price 5s. 6d. ; post free 6s.)

A catalogue of the most up-to-date books—and of those older titles still in demand—in the Ministry's main library, including a complete numerical list of Ministry bulletins, etc.

SPECIFICATIONS AND METHODS OF ANALYSIS FOR CERTAIN PESTICIDES. Ministry of Agriculture, Fisheries and Food. Tech. Bull. No. 1. Third edition. (London : H.M. Stationery Office. 1958. Pp. 122, illus. Price 7s. ; 7s. 6d. post free.)

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1. All **manuscripts** should be in double-spaced typewriting, with a good margin, and should be addressed to the Editor, East Malling Research Station, near Maidstone, Kent, England. Papers must be written concisely. Historical reviews should be as short as possible and only such references to literature as bear directly on the subject should be included. Tables and illustrations, if any, must be only such as are absolutely essential for clear presentation.

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3. Each paper must conclude with a concise and critically correct **summary** of its actual content. It should contain any new or verified constants as well as any other critical data of permanent value but not tables or graphs. Any organism mentioned should be given its scientific name.

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